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The First-Instar Larva of a Species of *Prosimulium*
(Diptera: Simuliidae)

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In the course of ecological work on black flies, some first-instar larvae that proved to be those of a species of *Prosimulium* were collected from trailing grass leaves in three streams in the Gatineau hills, seven miles north of Ottawa, in October, 1958. These larvae lack the head-fans (premandibular organs) characteristic of the later instars and of the larvae of most other black flies, and in this and other respects resemble those of *Gymnopais* Stone and *Twinnia* Stone and Jamnback. There is no reference in the literature to such a form and it seems clear that the first instar of *Prosimulium* was hitherto unknown.

The identity of the larvae was readily established. Five individuals were kept in the laboratory overnight and the following morning two had died while three had moulted to the second stage and now possessed fully formed head-fans. This second instar proved to be identical with the smallest *Prosimulium* larvae (1.0-2.0 mm. long) hitherto recognized from the streams in question. These streams were inhabited both by *P. fuscum* Syme and Davies and *P. mixtum* S. and D., two species forming part of the complex formerly included under the name *P. hirtipes* Fries (see Syme and Davies, 1958). Specific differences between the early larval instars of these forms have not been detected, but there is circumstantial evidence suggesting that the larvae to be described below are those of *P. fuscum*.

For comparison larvae of an undescribed species of *Gymnopais* from Anchorage, Alaska and of *Twinnia tibblesi* Stone and Jamnback, from Goose Bay, Labrador, were examined, The larvae of *Gymnopais* were kindly provided by Dr. K. M. Sommerman, Arctic Health Research Centre, Anchorage.

Length including head 0.7-0.9 mm.; body of normal form. Anal 'gills' consisting of three simple branches; anal sclerite not detected, but the cuticle of the anal area with minute spines as in later instars. Posterior attachment organ with two or three hooks in each radial row, the number of rows in the whole organ difficult to determine, approximately 50-60.

Head in dorsal view (Fig. 1) widest (0.14 mm.) close to posterior end, length about 0.20 mm., lightly sclerotized and pale yellow in life except for the black posterior collar, the dark brown mid-dorsal oval area surrounding the black egg-burster tooth, and the dark phragma behind the mandible; fronto-clypeal sutures meeting near the hind edge of the head capsule and extending anteriorly as shown in Fig. 1; eye-spots rather close to posterior edge of head capsule, which has a large ventral emargination (Fig. 2); antennae, antennal sockets and associated sensilla as shown in Fig. 1; beside the antennal sockets is a semi-oval transparent area with sharply defined limits, partly surrounded by a darkened extension of the mandibular phragma (Fig. 2).

The labrum is well developed and its structures are described in series from the dorsal to the ventral end of the labral complex as seen in optical section at a magnification of 1280 with phase contrast. A pair of bristles with conspicuous sockets (the hindmost of the three pairs shown at the anterior end of Fig. 1) lie

close to the mid-dorsal line and are seen simultaneously with a pair of pectinate bristles situated more laterally (Fig. 1). The median bristles appear to be homologous with the pair near the junction of the labral region and the fronto-clypeus in *Gymnopais* (Fig. 10) and in later instars of *Prosimulium* and *Simulium* sens. lat. (see Puri, 1925, Plate 9, Fig. 22). They form a useful landmark in comparative studies. The two-branched median plate-bearing structures, the uppermost of which is shown at the extreme front end in Fig. 1, are three in number. The second is almost directly below the uppermost and is shown in Fig. 3, while the third (Fig. 4) lies below and behind the second. Each plate droops ventrally and is concave below.

The remaining parts of the labral region form an upper-lip complex extending posteriorly towards the hypopharynx. Fig. 3 shows, in optical section, two bent rods associated with the base of the plate-bearing structures, and further back, a horseshoe-shaped refractile rod, with a terminal nodule visible in some slides (Fig. 3a). Fig. 4, an optical section in a plane ventral to that of Fig. 3, shows part of a pair of conspicuous curved bristles bearing long and slightly curved pectinations, situated in front of a quadrangular lobe which is terminated at each posterior corner by a sensillum of the basiconic type, and which bears small hair-carrying plates. Posterior and slightly dorsal to the quadrangular lobe is a tuft of stiff bristles, shown in Fig. 3.

The mandible (Fig. 5) is notable chiefly because of its curved terminal series of seven teeth and its slender shape, contrasting with the more flattened, blunt mandibles of typical black fly larvae (Rubtzov, 1956, Fig. 16) including those of the later instars in *Prosimulium*. The general form of the maxillae (Figs. 6, 6a) is normal. The bristle-bearing flaps on the ventral aspect of the maxillary lobe are three in number, but owing to close overlap only two are shown. The submentum (Fig. 7) has a nine-toothed central element; it is quite different in form to that of second instar (Fig. 8). The hypopharynx, shown in Fig. 9 in ventral view, is recognizably similar to that of typical black fly larvae. The bristle bundles shown in the figure are duplicated on the sloping dorsal surface also, but have been omitted for the sake of clarity. Such bristle bundles are a conspicuous feature of the hypopharynx in full grown larvae of *Simulium* (Puri, 1925; Plate 9, Fig. 25).

Discussion

The first instar of *Prosimulium* described above is probably of brief duration, since the larvae moulted within twelve hours of collection. This, coupled with the pronounced scatter in time of egg hatching and the small size of the larvae, might explain why this stage has not been found hitherto. It seems likely that first-instar larvae of the type described will prove to be the normal form in the genus *Prosimulium*. In a species of *Cnephia* (probably *C. mutata* Mall.) found in the same streams the first instar possesses head-fans, as it does also in *Simulium* sens. lat. (Puri, 1925).

The absence of head-fans, the pronounced tapering of the head capsule in dorsal view and the form of the fronto-clypeus give the first instar *Prosimulium* larva a characteristic facies resembling that of later larvae of *Gymnopais* and *Twinnia*. Certain details of the labrum emphasize this similarity. The labrum

Figs. 1-10. 1-7, 9. *Prosimulium* sp., first instar larva. 1, head in dorsal view; 2, head in lateral view; 3, labrum, optical section; 4, labrum, optical section ventral to that in 3; 5, right mandible, ventral view; 6, right maxilla, ventral view; 6a, right maxillary lobe, dorsal surface; 7, submentum; 9, hypopharynx, ventral view.   8, *Prosimulium* sp., second instar larva, sub-mentum. 10-10b, *Gymnopais* sp. 10, labrum of last instar larva, lateral view; 10a, lobe bear-ing sensilla; 10b, pectinate bristles.
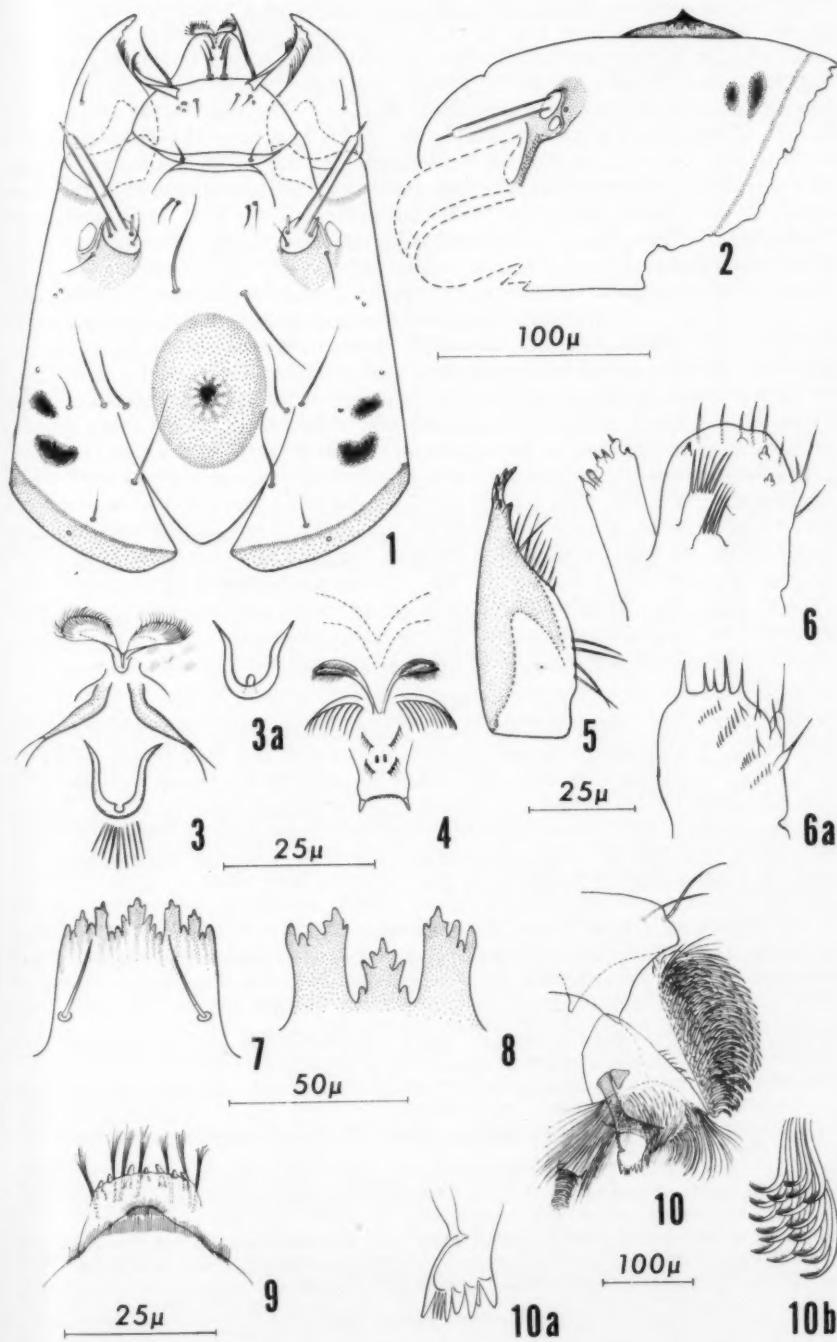
of *Gymnopais* is shown in Fig. 10, and that of *Twinnia* is broadly similar. A lobe bearing basiconic sensilla (Fig. 10a) is situated in a corresponding position to the lobe illustrated in Fig. 4 in *Prosimulium*. Furthermore, in the large anterior tract of thick curved bristles, the lower ones are pectinate (*Gymnopais*, Fig. 10b) or terminally serrate (*Twinnia*), and may correspond in part with the pair of pectinate bristles in *Prosimulium* (Fig. 4). The differences between the labrum of later-instar *Gymnopais* and that of the first-instar *Prosimulium* appear to be largely the result of the greater size and vastly increased numbers of bristles in the former. A more rewarding comparison would be that between the first-instar larva of both genera, but unfortunately this stage is as yet unknown in *Gymnopais*. These features of *Prosimulium* emphasize the relationship of the genus to *Gymnopais* and *Twinnia*, a position already well established by the work of Stone (1949), Sommerman (1953), Stone and Jamnback (1955) and Shewell (1958). Furthermore they confirm the idea that the characteristics of the latter two genera, whereby they differ from most other black fly larvae, are primitive features rather than secondary specializations.

Shewell (1958) has already drawn attention to the general chironomid-like facies of the larval head in *Gymnopais* and *Twinnia*. Certain details of the first-instar larvae of *Prosimulium* emphasize this similarity. In the labral complex, plates broadly similar to those shown in Fig. 3 are present in some Chironominae (Johannsen, 1905; Plate 21, Fig. 15) and a horseshoe-shaped rod is depicted for several chironomid larvae in the same work (Plate 23, Fig. 10) and by Lenz (1954, Figs. 50, 87). The ventral lobe of the hypopharynx bears fine regular bristles (Fig. 9) and is similar to that in some chironomids (Johannsen, 1905, Plate 21, Fig. 6). The finding of these larvae thus serves not only to integrate an aspect of our knowledge of the more primitive Simuliidae but also to indicate additional points of contact between that family and the Chironomidae.

Summary

The first-instar larva of a species of *Prosimulium*, probably *P. fuscum* Syme and Davies, is described. It differs from the second and later instars primarily in lacking head-fans. In this and other respects it resembles the larvae of *Gymnopais* and *Twinnia* and the findings confirm the suggested primitive position of these genera and the close relationship of *Prosimulium* to them. In some features of the labrum and hypopharynx the first instar of *Prosimulium* also resembles the larvae of certain Chironomidae.

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Four New Species of *Prosimulium* (Diptera: Simuliidae) from Western United States[1]

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During recent years intensive studies have been carried out on the black-fly fauna of Utah and of Wyoming by the senior author and junior author respectively. As a result of these investigations a number of new black-fly species were collected, four of which are described below.

The following descriptions and measurements were made from alcohol-preserved specimens, but where available, pinned, dried specimens were also used in preparation of the descriptions. Most of the drawings were made from slide mounts with the aid of a Ray-O-Scope microprojection apparatus; the others were made from cleared specimens retained in glycerin and were drawn with the aid of a squared-grid ocular in a stereoscopic microscope.

Prosimulium daviesi, new species

Prosimulium sp. 199, Peterson, 1959, Can. Ent. 91: 147.

Female. General color dark reddish- to orangish-brown. Length: body, 3.3-4.5 mm.; wing, 3.3-4.0 mm.

Head dark brown to black, densely covered with moderately long, golden-yellow hair. Eyes large, extending to top of vertex. Frons broad, strongly divergent above, width at apex of eyes slightly less than twice that of narrowest point; usually lighter than vertex and occiput; covered with moderately long, decumbent, golden-yellow hair. Clypeus somewhat longer than wide, strongly convex, yellowish-brown and usually lighter than frons; densely covered with moderately long, golden-yellow hair, interspersed with some stout, dark hair that may have pale tips. Antenna 11-segmented, yellowish-brown, scape and pedicel and base of third segment paler than rest; with short, proclinate, pale hair and a few stout dark hairs on outside margin of segments; flagellum about four times as long as scape and pedicel. Palpus yellowish-brown, third segment darker; with dense, moderately long, yellowish hair, sparse on distal segment; sensory vesicle of third segment somewhat less than one-half the length of the segment and is proximally situated; the tube leading from the sensory vesicle to the exterior arises from the distal portion of the vesicle and extends obliquely forward and upward, widens distally and terminates as an enlarged opening. Mandible with 38-42 fine serrations; galea of maxilla with 25-27 large, retrorse teeth. Median space of buccopharyngeal apparatus broad, of a squared U-shape; dorsolateral arms slender, heavily sclerotized, expanded dorsally into inwardly directed plates.

Pronotum and prescutum yellowish- to orangish-brown, with long, erect, golden-yellow hair. Scutum dark reddish- to orangish-brown, with dense, recumbent, golden hair that is longer on lateral and posterior margins; viewed from front, with two pale, slender, orangish vittae, one on either side, slightly curved laterally at posterior margin, curved laterally and slightly enlarged at

anterior margin; viewed from back, three narrow, dark vittae are visible; lateral margins of scutum mottled. Scutellum brownish-yellow, with long, golden-yellow hair, some with dark bases. Postscutellum mottled orangish-brown, shining, bare. Pleuron lighter than scutum, mottled; pleural membrane lighter, yellowish- to grayish-brown; pleural tuft of pale yellow hair. Wing veins yellowish; stem vein, base of costa, and undersurface of subcosta with pale yellow hair, some on costa with dark bases. Fringe of calypter and alar lobe pale yellow. Halter white to pale yellow, stem with fringe of short, pale hair. Legs brownish-yellow, distal ends of femora and both ends of the other segments and all tarsi darkened, coxae brown with yellow areas; segments covered with long, pale yellow hair, interspersed with some dark hair on apices of segments and especially on tarsi; hind basitarsus about 6.4 times as long as wide; second hind tarsal segment about 4.5 times as long as wide; claws simple.

Abdomen dark yellowish- to grayish-brown, lighter on anterolateral and ventral regions; tergal plates not reduced, black on posterior margins; segments with short, pale yellow hair, and with some dark hair on posterior segments; sternites 1-7 membranous, 8 with a sclerotized plate; fringe of basal scale yellow. Anal lobe (Fig. 3) narrow dorsally, broad ventrally, produced posteriorly and to a lesser extent anteriorly; posterior margin sclerotized; densely setose. Cercus rectangular, twice as broad as long; densely setose, a few females show one extra large seta on a slightly raised tubercle (Fig. 3). Ovipositor flaps short, not reaching tip of anal lobe, densely setose; outside margin rounded, tapering to a rounded apex; inner margin densely but narrowly sclerotized, concave basally, convergent apically (Fig. 2). Genital rod short, broadening towards arms; arms narrow, strongly divergent, a right-angle bend occurring just before they expand into large, concave, C-shaped plates each of which has a long inner prolongation, those of the two plates nearly touching (Fig. 1).

Male. Similar in size to female; general body color darker blackish-brown.

Posterior margin of head, medial marginal area between eyes, frons and clypeus with moderately long, erect, dark hair, some with pale tips, and interspersed with some entirely yellow hair; undersurface of head with long, pale yellow hair interspersed with some stout, dark hair. Antenna yellowish- to orangish-brown, three basal segments often darker than others; segments covered with short, proclinate, yellow hair, interspersed with a few longer, dark, stout hairs especially on basal three segments; second segment largest, flagellum about four times as long as scape and pedicel. Palpus yellowish-brown, slightly lighter than antenna, segments 3 and 4 darker than others, all with dark hair interspersed with some pale hair.

Pronotum and prescutum dark yellowish- to orangish-brown, with long, golden-yellow hair. Scutum dark orangish- to blackish-brown, densely covered with recumbent, golden-yellow hair that is longer and paler on anterior, lateral and posterior margins, hair on posterior region erect. Scutellum yellowish-brown, with long, erect, golden hair. Postscutellum orangish-brown, lighter than scutum, shining and bare. Pleuron yellowish-brown; pleural membrane yellowish- to grayish-brown; pleural tuft elongate, yellow. Wing veins yellowish; hair of stem vein, base of costa, and fringe of calypter and alar lobe yellow; undersurface of subcosta with dark hair. Halter white to pale yellow apically, stem brown. Legs yellowish-brown, distal ends of femora and both ends of other segments and tarsi darkened; segments covered with long, yellow hair, interspersed with dark hair especially on tarsi; hind basitarsus 4.0-4.5 times as long as greatest width; second hind tarsal segment about 2.7 times as long as wide.

Abdomen brown dorsally, darker on segments 6-9; tergal plates sclerotized, not reduced, yellowish-brown with a narrow, dark band followed by a narrow, gray band; sternites dark brown, heavily sclerotized except for 2 and 3; anterior ventral regions of abdomen yellowish-brown; segments densely covered with short, yellow hair dorsally, sternites with long, yellow to brownish-yellow hair; basal scale with fringe of very long, fine, yellow hair that have dark bases. Basistyle large, about as broad basally as long, narrowed distally, about as long or slightly longer than dististyle. Dististyle slightly curved medially, broad basally, tapering apically, terminating with two stout spines (Fig. 6). Ventral plate wide basally, about one-half as wide apically; apex triangular with a somewhat flattened face and sides, and flattened or slightly concave on dorsal margin, shallowly concave behind apical margin; basal arms short, bluntly pointed (Figs. 4, 5). Paramer short and broad, roughly triangular in shape. Median sclerite Y-shaped, stem very short, arms much longer and narrower, not strongly divergent.

Pupa (Fig. 12). Length, 3.5-5.0 mm. Respiratory organ, 2.0-2.5 mm. long, slightly longer than dorsum of head and thorax; with 16 filaments arising from three well separated, main trunks that in turn arise from a short petiole; the dorsomedial trunk divides into three branches, an inner with three filaments, a dorsal with two filaments, and an outer with three filaments, eight filaments total; the dorsolateral and ventral trunks each give rise to four paired filaments (Fig. 11). Head and thorax lightly rugose; thorax with six stout, dorsal trichomes, and several lateral trichomes. Tergites 1 and 2 with a variable row of setae; 3 and 4 with eight large hooks on posterior margin; 5-9 with a single row of fine spines on anterior margin; posterior margin of 5-8 usually with a variable row of setae, those of segment 8 longer and stouter; terminal spines anteriorly directed, separated and strongly divergent apically, each with a stout seta at the base both in front and behind. Sternites 4-7 each with four hooks on posterior margin, these increasingly larger and farther apart on the more posterior segments; sternites 8 and 9 with scattered setae. Cocoon a loosely woven sock, covering little more than the abdomen of pupa.

Larva. Mature specimens 8.0-8.5 mm. long. Head capsule dark orangish-brown, faintly mottled with lighter and darker areas, posterior margin darkened. The head-spot pattern shows considerable variation in color intensity; head spots brown, anterior and posterior median groups widely separated but usually connected by a narrow, dark line, anterolateral and mediolateral groups usually distinct, a moderately large, light area usually occurs on each side posterior to mediolateral spots; head spots surrounded by a darkened fulvous area that is triangular in shape and extends forward on frontoclypeal plate to a position opposite the posterodorsal arms of the mandibular phragma; a small light spot, from which one or two short setae project, occurs on the lighter portion of the frontoclypeal plate anterior and mesad of base of antennae. Epicranial plate dark orangish-brown; ventral arm of mandibular phragma short, both arms heavily sclerotized. Throat cleft (Fig. 9) rectangular, slightly narrowed and rounded apically, somewhat wider than long, extends forward about one-third the distance to base of submentum. Submentum heavily sclerotized anteriorly; the median trifid tooth is usually somewhat longer than the last lateral teeth which in turn are longer than the other lateral teeth (the length of the submental teeth is variable as is the degree of lateral curvature of the outer lateral teeth, see Figs. 7, 8); one long and three or four short epicranial setae on each side; distance from apex of outermost tooth of submentum to base of anteriormost epicranial seta on same side considerably less than the distance between apices of outermost teeth; lateral margins with prominent serrations. Mandible (Fig. 10) with small teeth

having relative lengths of about 6-4-9 from distalmost basad, the middle tooth less heavily sclerotized than other two and is often difficult to see; these followed by about ten bristle-like teeth; inner subapical margin with 13-16 teeth whose bases are nearly in a straight line, the first three or four teeth more prominent but subequal in size. Maxillary palp dark except for apical one-third which is color-less, about three times as long as greatest width at base; palp with a number of scattered, long, spine-like setae. Relative lengths of antennal segments, from base to apex, 6-10-7.5-1; two apical segments dark brown. Cephalic fan with about 25 rays. Pupal respiratory histoblasts with 16 filaments.

Abdomen of preserved specimens brownish-gray with lighter interseg-mental lines. Anal gill of three simple lobes. Anal cross-piece with arms heavily sclerotized, area between arms broad, moderately sclerotized; ventral arms nearly straight, slightly shorter and more slender than the curved, dorsal arms; a small patch of short setae occurs at posterior margins of dorsal arms. Anal hooks nine or 10 per row, in about 75 rows.

Holotype. Female (reared) (genitalia mounted on slide); small stream 19.3 miles up Logan Canyon, Cache County, Utah, elevation 6,200 feet, May 26, 1957, B. V. Peterson; deposited in the U.S. National Museum.

Allotype. Male (reared); same data as for holotype.

Paratypes. One reared male (genitalia on slide), one reared female (head and genitalia on slides), and one pupal skin, same data as for types; one male, head of Weber Canyon, Morgan County, Utah, May 26, 1958, B. V. Peterson; eight pupal skins, 3 miles northeast Mirror Lake, Duchesne County, Utah, elevation 10,050 feet, September 1, 1957, B. V. Peterson; numerous mature larvae and one pupa, Fox Creek-Fence Creek confluence, Albany County, Wyoming, elevation 7,500 feet, May 8, 1956; two males, three females (reared) (pinned dry), pupae, mature larvae, same data except collected May 23, 1956, adults emerged May 24-27, 1956; mature larvae, same data except collected May 20, 1956, all G. R. DeFoliart; one male (reared), three pupae, mature larvae, first small stream above Albany, Albany County, Wyoming, June 20, 1957; five males (reared), six females (reared), four pupae and three larvae, same data except collected June 11, 1958, adults emerged June 12-15, 1958, all G. R. DeFoliart; eight females (reared) (pinned dry), pupae, mature larvae, Lake Creek, 12 miles southeast of Alpine, Lincoln County, Wyoming, June 26, 1957, adults emerged June 26-29, 1957, G. R. DeFoliart; one female (reared), small stream about 7 miles south of Smoot, Lincoln County, Wyoming, June 15, 1958, G. R. DeFoliart. Paratypes deposited in the collection at the U.S. National Museum, University of Utah, University of Wyoming, University of Wisconsin, and the Canadian National Collection.

This species is named in honor of Dr. Douglas M. Davies, of McMaster University, Hamilton, Ontario, who has added considerably to the knowledge of the biology of the black flies of eastern North America.

Comparison With Related Species

Adults of *Prosimulium daviesi* resemble those of the "*hirtipes*" complex. Syme and Davies (1958) divided the North American *hirtipes* into three species, *P. fuscum*, *P. mixtum*, and *P. fontanum*. Of these, *P. daviesi* most closely resembles *P. fontanum*, but may be distinguished from it by the larger size and more orangish color of the integument of both sexes; the strongly convex clypeus, pale pubescence of antennae, sensory vesicle of the palp with a distinct tube leading to the outside, two faint vittae on scutum, and shape of the genital
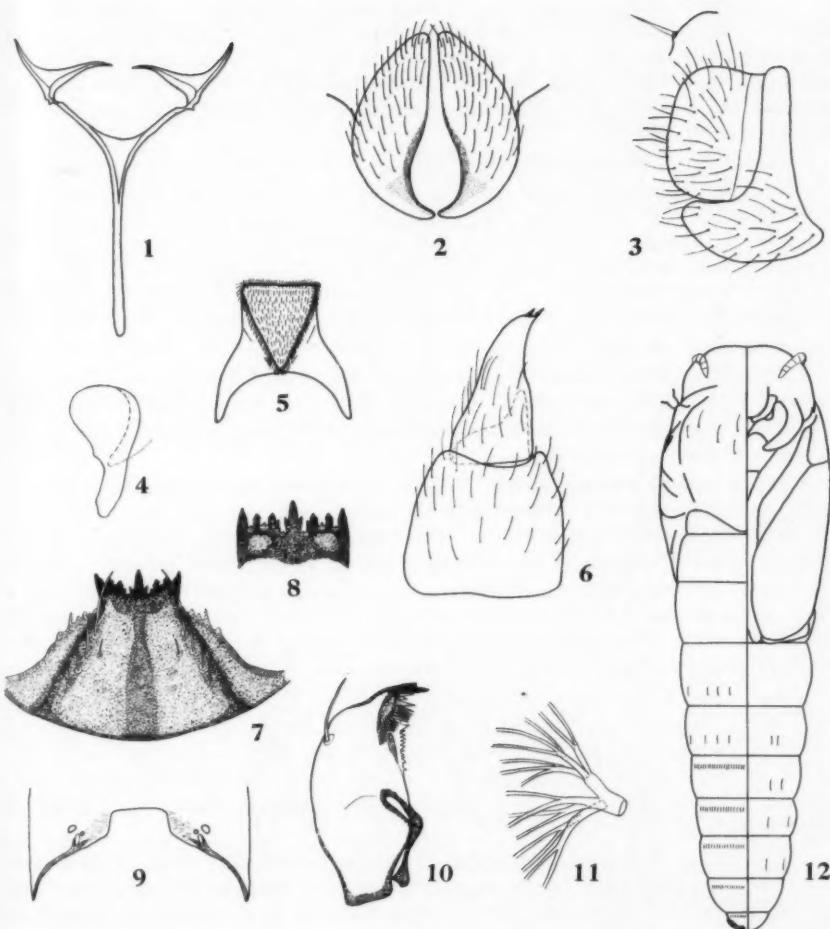
Figs. 1-12. *Prosimulium daviesi*, n.sp. Figs. 1-3, female. 1, genital rod; 2, ovipositor; 3, right anal lobe and cercus. Figs. 4-6, male. 4, ventral plate, lateral; 5, ventral plate, ventral; 6, left basistyle and dististyle, outer surfaces. Figs. 7-10, mature larva. 7, submentum; 8, submental teeth, illustrating variability in length of submental teeth and the degree of lateral curvature of the outer lateral teeth (compare with Fig. 7); 9, throat cleft; 10, right mandible. Figs. 11-12, pupa. 11, left respiratory organ, outer surface; 12, pupa: left side, dorsal; right side, ventral.

rod of the female. Males of *P. daviesi* differ from those of *P. fontanum* by the yellow hair on the stem vein and base of costa, white to pale yellow halter, paler legs, yellow hair on legs more extensive, yellow hair dorsally on abdomen, hair of basal fringe yellow with dark bases, and the shape of the ventral plate.

Pupae of the two species are very similar, each having a respiratory organ of 16 filaments with the same pattern of branching. Pupal chaetotaxy is essentially the same. Larvae of the two species are also very similar but those of *P. daviesi* tend to be larger and have a more orangish-brown head capsule.

The more orangish color of the integument, the convex clypeus, and the shape of the genital rod and ovipositor flaps distinguish females of *P. daviesi* from those of *P. fuscum* and *P. mixtum*. The lighter yellowish-brown legs with more extensive yellow hair, the paler brown antennae with pale hair, and the shape of the ventral plate will distinguish males of *P. daviesi* from males of *P. fuscum* and *P. mixtum*.

Larvae of *P. daviesi* are similar to those of *P. fuscum* but the median trifid tooth of the submentum often exceeds the length of the lateral teeth which in *P. fuscum* may be as high but does not exceed the lateral teeth. The subapical ridge of the mandible of *P. fuscum* and *P. mixtum* has 12-20 forward-pointing teeth, whereas those of *P. daviesi* vary from 13-16, have their bases in nearly a straight line and with the teeth perpendicular to the bases. Larvae of *P. daviesi* are generally lighter, have a more orangish colored head capsule, and are larger than those of *P. mixtum*.

Females of *Prosimulium hirtipes* (Fries) from North Europe, as defined by L. Davies (1957), differs from *P. daviesi* by their dark grayish-black color, dark legs, claws with a minute basal tooth, entirely black antennae, and shape of the genital rod and ovipositor flaps.

Prosimulium inflatum Davies, a species recently separated from the European *hirtipes* (L. Davies, 1957), differs from *P. daviesi* by its darker color, gray frons, black antennae, dark halters, claws with minute basal tooth, and shape of the genital rod and ovipositor flaps. The pupa of *P. inflatum* has no hooks on sternite 4, whereas sternite 4 of *P. daviesi* possesses four small hooks. The larva of *P. inflatum* has a black to dark brown head capsule with an indeterminable dorsal pattern. The larval head capsule of *P. daviesi* is lighter orangish-brown and the head spot pattern is usually distinguishable.

Rubtzov (1956) described three varieties of *P. hirtipes*, *hirtipes* (Fries), *luganicum* Rubz., and *diminutum* Rubz., from the U.S.S.R. Comparison of Rubtzov's illustrations show that all three varieties differ from *P. daviesi* in the shape of the male and female genitalia and the larval submentum. Pupae of *P. hirtipes hirtipes* have respiratory filaments that differ in shape and pattern of branching from that of *P. daviesi*.

The adults of *Prosimulium travisi* Stone closely resemble those of *P. daviesi*. However, the adults can be distinguished from *P. daviesi* by the ashy-gray sides of the thorax and abdomen, and the male genitalia of *P. travisi*, as figured by Sommerman (1958) are quite distinct from that of *P. daviesi*. The pupae of the two species are readily separated by the closely clumped respiratory filaments and the strongly rugose head and thorax of *P. travisi* as opposed to the more widespread filaments and the nearly smooth head and thorax of *P. daviesi*. Sternite 4 of the pupa of *P. travisi* bears two hooks ventrally while that of the pupa of *P. daviesi* has four hooks.

Females of *Prosimulium ursinum* (Edwards) differ from *P. daviesi* by their poorly sclerotized and weakly toothed mandibles and maxillae, abdominal sternites 2-6 are heavily sclerotized, the claw bears a minute sub-basal tooth and by the shape of the genital rod. According to L. Davies (1954), females of *P. ursinum* are fully gravid upon emergence from the pupa, whereas the females of *P. daviesi* contain only very small eggs in the ovaries at the time of emergence. Males of *P. ursinum* were not available for study, but Dr. Stone (in litt., 1958) mentioned that they were difficult to distinguish from *P. daviesi*. However, judging from the illustrations of *P. ursinum* by Syme and Davies (1958), there is a distinct difference in the shape of the ventral plate of the two species. The

pupa of *P. ursinum* has a respiratory organ with 14 filaments as opposed to 16 filaments for *P. daviesi*.

Females of both *Prosimulium rhizophorum* Stone and Jamnback, and *P. saltus* Stone and Jamnback, have claws that bear a minute basal tooth, a feature that is not present in *P. daviesi*. Also, females of *P. saltus* are generally more blackish-brown in color. Judging from Stone and Jamnback's (1955) descriptions of their two species, the genital rods are considerably different from that of *P. daviesi*. The pupae of both *P. rhizophorum* and *P. saltus* are readily distinguished from *P. daviesi* by the form of their respiratory organs.

Prosimulium exigens Dyar and Shannon can be distinguished easily from *P. daviesi* on the basis of the male and female genitalia. Also the pupal respiratory organs immediately separate the two species as does the submentum of the larvae.

Prosimulium frohnei Sommerman is distinguished from *P. daviesi* by its darker color and silvery pubescence of the female and male; structure of the male genitalia; shape and number of filaments of the pupal respiratory organ; and by the dorsal head pattern, complete mandibular phragma, and shape of the sub-mentum and throat cleft of the larva.

Both *Prosimulium perspicuum* Sommerman and *P. alpestre* Dorogostajsky, Rubtzov and Vlasenko have only bristle-like projections on the maxillae of the females in contrast to the large retrorse teeth on the maxillae of females of *P. daviesi*. Again, the structure of male genitalia serves to distinguish the males of the three species.

Biology

Little is known of the biology of *P. daviesi*. In Utah, the species was first collected in a small stream in Logan Canyon, elevation 6,200 feet, May 26, 1957. This stream was about 12 inches wide and four to six inches deep, with a current velocity varying from one to three feet per second. The water temperature was 55° F. The stream bottom was of packed mud and gravel with a few scattered larger rocks. Aquatic vegetation was in abundance, as were grasses along the stream's edges. The pupae and larvae occurred in small groups, or singly, on the top of small rocks, and on grass blades trailing in the water. Pupal skins taken three miles northeast of Mirror Lake, elevation 10,050 feet, were found on the undersides of small rocks in a narrow stream that ran through a grassy, alpine meadow.

A single male was taken on the wing while flying with a small swarm of *P. exigens* males and females on May 23, 1958, at the head of Weber Canyon, Utah.

In Wyoming, the species has been found to be widely distributed in the mountainous regions, usually at elevations of 7,000 feet or higher. It was found most frequently in streams on the east side of the Medicine Bow Mountains in southeastern Wyoming and in the Salt Range in the west, but it has been found also in the Wind River Range and as far north as Togwotee Pass. Larvae and pupae were generally found in shaded, fast-flowing, permanent or temporary streams varying in width from about one to eight or 10 feet. They were attached to submerged rocks, twigs or dead leaves.

Prosimulium uinta, new species

Female. General color dark reddish-brown to blackish-brown. Length: body, 3.0–4.0 mm.; wing, 3.0–3.5 mm.

Head densely covered with moderately long, decumbent, yellow hair, with a somewhat irregular row of long, stout, black hairs along posterior and lateral

margin of eye. Eyes rather small, not extending to top of vertex. Frons only moderately broad, sides moderately divergent above, covered with short, yellow hair. Clypeus slightly paler than frons, somewhat longer than broad, sparsely covered with yellow hair that becomes more dense on ventral portion and is directed medioventrally. Antenna 11-segmented, short, dark brown, basal two segments darker than others; covered with short, pale hair; basal segments broad, gradually tapering apically, second and third segments subequal in size, flagellum about three times as long as scape and pedicel. Palpus brown, third segment darker; with fine, pale hair intermixed with stouter, dark hair; segments 3 and 5 equal in length, 4 shorter. Sensory vesicle of third segment considerably less than one-half the total length of segment; tube leading to the exterior uniformly broad, arising near distal end of sensory vesicle; the vesicle itself is situated in proximal portion of segment. Mandible with about 50 serrations; galea of maxilla with about 29 retrorse teeth. Median space of buccopharyngeal apparatus deep, narrowly V-shaped; dorsolateral arms long, slender, heavily sclerotized, inwardly directed at apex.

Pronotum and prescutum only faintly lighter than scutum; pronotum with long, erect, pale yellow hair. Scutum densely covered with moderately long, recumbent, yellow hair, that is longer on posterior margins. Scutellum slightly lighter than scutum, with erect, yellow hair. Postscutellum dark brown, bare, shining. Pleuron slightly lighter and more reddish than scutum; pleural membrane reddish- to yellowish-brown; pleural tuft of long, yellow hair. Wing veins yellowish; hair on base of costa, stem vein and undersurface of subcosta yellow. Fringe of calypter and alar lobe pale yellow. Halter yellowish-brown. Legs rather dark yellowish- to reddish-brown, ends of segments and tarsi darker (more evident in alcohol material); covered with moderately long, yellow hair, that of tarsi more brownish; hind basitarsus about four times as long as greatest width; second hind tarsal segment three to four times as long as wide; claws short, slender, simple.

Abdomen dark brown to reddish-brown; tergal plates 3-6 somewhat reduced and about equal in size, moderately sclerotized, reddish centrally, surrounded by dark brown, posterior margin gray; covered with short yellow hair; hair longer and more dense on lateral margins of abdomen; sternites broad, all lightly sclerotized except for the second which is membranous, 8th broadly U-shaped, heavily sclerotized especially along distal margin; sternites sparsely covered with short, pale hair, intermixed with some dark hair; basal scale with fringe of long, yellow hair. Anal lobe broad, somewhat L-shaped, posterior ventral margin with numerous long, fine setae, moderately setose elsewhere. Cercus rectangular, slightly less than three times as broad as long, moderately setose (Fig. 14). Ovipositor flaps broadly rounded basally, tapering distally, apex acutely rounded; broadly sclerotized on inner margins; moderately setose; reaching tip of anal lobe (Fig. 15). Genital rod long and slender; arms short, slender, widely divergent, expand apically into moderately broad plates each with a short, medial projection (Fig. 13).

Male. Similar in size to female but generally darker in color.

Posterior and undersurface of head, medial marginal area between eyes, frons and clypeus with brownish-yellow hair. Antenna short; dark brown, basal two segments darker than others; with short brownish hair; segment 2 the broadest, 3 the longest, flagellum about four times as long as scape and pedicel. Palpus brown, third segment long, slender and darker than others; covered with moderately long, brown hair.

Scutum blackish-brown, somewhat darker than in female, covered with moderately long, yellow hair, three faint pale vittae visible, all slender, median one straight and of uniform width, lateral vittae terminate as enlarged pale areas at humeral angles. Scutellum slightly lighter than scutum, with long, erect, yellow hair. Postscutellum dark, bare, shining. Pleuron dark; pleural membrane yellowish- to grayish-brown; pleural tuft yellow. Wing veins yellowish; long hair on base of costa mostly yellow, but with a few stout, dark hairs; stem vein with yellow hair. Fringe of calypter and alar lobe pale. Halter brown. Legs as in female; hind basitarsus about 3.5 times as long as greatest width; second hind tarsal segment only one-third longer than wide.

Abdomen dark blackish-brown; tergites broad, 2-5 slightly more narrow than others, all sclerotized, sparsely covered with short, brownish-yellow hair; sternites lightly sclerotized, moderately broad, with patches of moderately long, brownish-yellow hair. Basistyle large, subquadrate, tapering distally to about one-half the width at base, greatest width equal to greatest length, moderately setose. Dististyle short, slightly more than one-half the length of basistyle, width at base more than one-half total length of dististyle; tapering to a somewhat rounded apex with three short, stout, terminal spines; moderately setose (Fig. 16). Ventral plate moderately broad; with a short, ventral, median projection that is triangular in shape and laterally compressed; basal arms short, broadly rounded and heavily sclerotized terminally (Figs. 17, 18). Parameral arm slender and curved, terminating in an elongate, flattened plate with rounded apex, heavily sclerotized. Median sclerite Y-shaped, stem very short and broad, arms slightly longer and more slender.

Pupa. Length, 3.0-4.0 mm. Respiratory organ 1.5-2.5 mm. long; consisting of 21-24 (average 22) filaments arising from three main groups of branches; each main group composed of two and occasionally three sub-branches which arise from a common short petiole; all the main groups arise from a short rounded knob (Fig. 19). Head and thorax densely covered with minute rounded tubercles; thoracic trichomes rather short, moderately stout, about three on each side. Tergite 2 with four very small setae along posterior margin of each side; 3 and 4 with eight large hooks on posterior margin; 5-9 with a row of short, stout spines along anterior margin; posterior margin of 8 with a row of about ten moderately long, fine setae. Terminal spines long, slender, and rather sinuous, somewhat reclined and anteriorly directed, strongly divergent apically, each with a stout seta at base, both before and behind. Sternites 4-7 each with four hooks, those of 4 smaller, those of 6 and 7 more widely separated along segment; sternites 8 and 9 bare except for scattered setae. Cocoon a loosely woven sock that covers entire pupa except the respiratory filaments.

Larva. Mature specimens 6.5-7.0 mm. long. Head capsule dark brown, frontoclypeal plate with pattern indistinct; head spots dark brown, anterior and posterior median groups separated by a narrow isthmus, to each side of which are the mediolateral head spots, a slightly darkened area narrowly surrounds the head spots; posterior margin darkened; a number of short scattered setae cover frontoclypeal plate. Epicranial plate dark, one or two small light spots ventral and posterior to eyes; a narrow pale area extends between apex of throat cleft and base of submentum. Throat cleft shallow, rectangular, sides nearly parallel, about twice as wide as long, extends anteriorly about one-fourth the distance from posterior margin to base of submentum. Subesophageal ganglion pale white. Submentum (Fig. 21) moderately sclerotized; lateral teeth of each side separated from median tooth by a distinct deep gap, the three main lateral teeth

of each side about equal in length or becoming slightly longer inwardly, about equal in length to median tooth; secondary projections of median tooth basal, extending slightly more than one-half length of median tooth; lateral margins with 7 or 8 serrations; one long and one or two short epicranial setae on each side. Distance from apex of outermost tooth to base of anteriormost epicranial seta on same side slightly less than distance between apices of outermost teeth. Mandible with small teeth having relative lengths of about 7-5-9 from distalmost basad, all three rather long, slender, and lightly pigmented; inner subapical margin with 8-12 very small teeth, the distalmost being the largest (Fig. 20). Maxillary palp short, slightly more than twice as long as broad. Antenna short, only slightly longer than stalk of cephalic fan, relative lengths of antennal segments, from base to apex, 12.5-19-15-2; two terminal segments pigmented. Cephalic fan with about 55 rays. Pupal respiratory histoblasts with 21-24 (average 22) filaments.

Abdomen of preserved specimens grayish-brown with lighter intersegmental lines. Anal gill of three simple lobes. Anal cross-piece heavily sclerotized, area between arms lightly so; dorsal arms somewhat longer than ventral arms. Anal hooks about nine per row, in about 84 rows.

Holotype. Male (reared) (genitalia on slide); Sweeney Creek, Skyline Drive, mile 8.4, Pinedale, Sublette County, Wyoming, June 26, 1957, emerged June 27, 1957, G. R. DeFoliart; deposited in the U.S. National Museum.

Allotype. Female (reared and with associated larval head capsule) (mounted on five slides); Chalk Creek Canyon, Uinta County, Wyoming, elevation 7,000 feet, May 17, 1958, B. V. Peterson; deposited in the U.S. National Museum.

Paratypes. One male (reared) (mounted on three slides), one male (reared) (genitalia on slide), one female (reared) (mounted on five slides), same data as for allotype; four pupae, Chalk Creek Canyon, Summit County, Utah, elevation 6,800 feet, May 17, 1958, B. V. Peterson; two females (reared) (pinned dry), six pupae and one mature larva, same data as for holotype. Paratypes deposited in the collection of the University of Utah, University of Wyoming, University of Wisconsin, and the Canadian National Collection.

Non-paratypic material. Fifteen larvae, not fully mature, Chalk Creek Canyon, Summit County, Utah, elevation 6,800 feet, May 17, 1958, B. V. Peterson.

Comparison with Related Species

Prosimulium uinta superficially resembles *P. exigens* in both sexes, but the genitalia provide reliable characters for separation of the two species. The genital rod of *P. uinta* has longer and more slender arms than the genital rod of *P. exigens*, and the ovipositor flaps are more broadly rounded basally and more narrow apically than those of *P. exigens*. The male genitalia of the two species are similar, each having a short dististyle with three terminal spines (sometimes four in *P. exigens*); however, the dististyle of *P. exigens* is considerably more narrow distally. The paramer of *P. uinta* is elongate while that of *P. exigens* is shorter and more rounded. The greatest difference in the male genitalia is provided by the ventral plate. That of *exigens* has a prominent, laterally compressed, median keel; whereas the ventral plate of *uinta* has a short, triangular, median projection that is less compressed laterally. The male of *P. exigens* has dark hair on the stem vein of the wing, but this is yellow in *P. uinta*. The general body vestiture of the female of *P. uinta* is a paler yellow than that of *P. exigens* which is more golden-yellow.
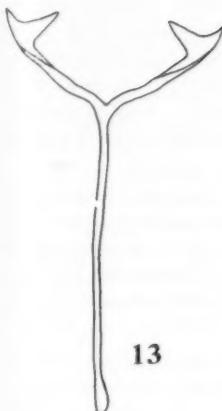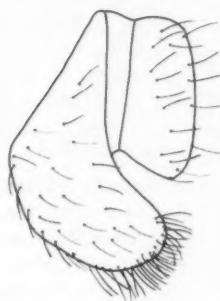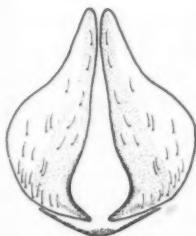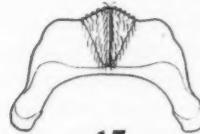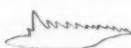
Figs. 13-21. *Prosimulium uinta*, n.sp. Figs. 13-15, female. 13, genital rod; 14, left anal lobe and cercus; 15, ovipositor. Figs. 16-18, male. 16, left basistyle and dististyle, outer surfaces; 17, ventral plate, ventral; 18, ventral plate, anterolateral. Fig. 19, left respiratory organ of pupa, outer surface. Figs. 20-21, mature larva. 20, subapical ridge of mandible; 21, submental teeth.

The pupae of the two species have short respiratory filaments, numbering 80-110 or more in *P. exigens*, and 21-24 in *P. uinta*. The larvae of these two species bear very close resemblance; the best distinguishing feature being found in the structure of the submental teeth. In *P. uinta* the lateral teeth on each side of the submentum are separated from the median trifid tooth by a distinct, deep gap, and the median tooth is about equal in length to the lateral teeth. In *P. exigens* there is little or no gap between the median and lateral submental teeth, and the median tooth is much longer than any of the lateral teeth.

Females of *Prosimulium dicum* Dyar and Shannon resemble those of *P. uinta* but differ in having dark hair on the stem vein, body hair more golden-yellow,

broader frons, larger eyes which extend to the top of the vertex, brighter yellow legs, and by the shape of the genitalia, particularly of the genital rod. The genitalia serve to separate the males. The pupa of *dicum* has a strongly rugose head and thorax, while the head and thorax of *uinta* are densely covered with minute, rounded tubercles that provide a roughened appearance. The respiratory organ of *dicum* is similar to that of *P. exigens* with numerous, fine filaments, while that of *uinta* has fewer and stouter filaments.

The pupa of *Prosimulium flaviantennus* (Stains and Knowlton) has 20-26 (average 25) respiratory filaments that arise from four or five main groups. The filaments of *P. uinta* arise from three main basal groups with an average of 22 filaments. Sternite 3 of *P. uinta* is bare, while that of *P. flaviantennus* has two small hooks. Adults of *P. flaviantennus* are immediately distinguished by their bright-yellow antennae and legs.

The pupa of *Prosimulium pleurale* Malloch differs from the pupa of *P. uinta* by its smooth head and thorax, possession of a row of fine spines on tergite 4, and a respiratory organ with an average of 26 filaments. The females of *P. pleurale* are immediately differentiated from *P. uinta* by the large basal projection on the claw and the three pleural patches of hair.

The pupa of the eastern species *Prosimulium magnum* Dyar and Shannon has a respiratory organ with 25-30 filaments. The shape and pattern of branching of this organ, and the presence of six slender hooks on sternite 3 separate it from *P. uinta*. The enlarged first flagellar segment of the antenna of the adult male and female of *P. magnum*, and the genitalia of both sexes easily separate the species from *P. uinta*.

Adults of *Prosimulium multidentatum* (Twinn), another eastern species, can be distinguished from those of *P. uinta* on the basis of genitalia in both sexes. The pupa of *P. multidentatum* possesses 23-28 (average 26) respiratory filaments compared to 21-24 (average 22) for *P. uinta*, those of the latter species are short.

Biology

Immature stages of *Prosimulium uinta* were collected from two small, spring-fed streams that varied from eight to 24 inches in width, and from two to four inches in depth. The mud bottoms of the streams were strewn with small rocks, and each stream supported a heavy crop of an aquatic grass. The water flow was very slow, and in some places showed no perceptible movement. The water temperature of each stream was 66° F. A few pupae and larvae of *P. uinta* were found associated with a few of those of *P. exigens*. Both the larvae and pupae were found attached to the upper sides of the blades of aquatic vegetation.

Prosimulium shewelli, new species

Female. General color dark orangish-brown. Length: body, 3.3 mm.; wing, 2.8 mm.

Head densely covered with moderately long, yellow hair, interspersed with a few longer, more erect, stout, dark hairs; a row of stout, dark hair along posterior and lateral margins of eyes. Eyes rather small, not extending to top of vertex. Frons broad, moderately divergent above, ratio of narrowest width to greatest width 7:10, length slightly shorter than greatest width, 8:10; slightly concave just above antennae; moderately covered with recumbent, yellow hair. Clypeus rather spherical in outline, about as wide as long, somewhat convex; sparsely covered with medioventrally directed, recumbent, yellow hair, ventro-

lateral margins with about six erect, stout, dark hairs. Antenna 11-segmented, short, segments broad; dark yellowish-brown, pedicel darkest; with pale yellow hair, and a few stout, black hairs; second segment largest, flagellum about 3.5 times as long as scape and pedicel. Palpus yellowish-brown, with segment 3 and the dorsal surface of 4 dark brown; with pale yellow hair, interspersed with some longer, stout, dark hairs; sensory vesicle less than one-half the length of segment, proximally situated and close to the dorsal surface of segment; the opening of the sensory vesicle to the exterior arises dorsally from distal tip of vesicle with almost no connecting tube. Mandible with about 37 serrations; galea of maxilla with about 26 retrorse teeth. Median space of buccopharyngeal apparatus a moderately deep, narrow, U- or V-shape; dorsolateral arms moderately long, broad, rounded dorsally, inner surfaces with a narrow, sclerotized ridge that terminates dorsally as a slight, medial projection.

Pronotum and prescutum faintly lighter than scutum, both with moderately long, pale-yellow, erect or semi-erect hair. Scutum dark orangish-brown; densely covered with short, recumbent, yellow hair that is longer and more erect on the anterolateral margin and posterior region; two pale, comma-shaped vittae visible on alcohol-preserved material. Scutellum, brownish-yellow, with dense, erect, yellow hair. Postscutellum orangish-brown, bare, shining. Pleuron lighter than scutum, pleural membrane yellowish gray-brown; pleural tuft small, pale yellow. Wing veins light yellowish-brown, the two rami of the radial sector long but lying close together; hair on stem vein and base of costa yellow; sub-costa with a few dark hairs distally on dorsal surface and a double row along most of the length of undersurface. Fringe of calypter and alar lobe yellow. Halter pale yellow. Legs yellowish-brown; coxae, trochanters, distal ends of femora, both ends of tibiae, and tarsi darkened; segments covered with short, yellow hair with a few scattered, long yellow hairs; some stouter, dark hair ventrally on the distal portion of the femora; tarsi with mixed light and dark hair; hind basitarsus about six times as long as wide; second hind tarsal segment about three times as long as wide; claws simple.

Abdomen infuscate, more yellow ventrally especially on anterior region; with short, yellow hair dorsally and some longer dark hair ventrally; tergites 2-6 slightly reduced; sternites 1-6 membranous, 7 lightly sclerotized, 8 densely sclerotized and broadly U-shaped; basal scale dark brown, with fringe of long, fine, yellow hair. Anal lobe narrow dorsally, broad ventrally, only slightly produced posteriorly, moderately setose. Cercus quadrate, about one-fourth wider than long, moderately setose (Fig. 24). Ovipositor flaps short, not reaching tip of anal lobe, broadly rounded basally on outer margin, tapering to a rounded apex; inner margin broadly concave basally, convergent distally, densely sclerotized; flaps moderately setose (Fig. 23). Stem of genital rod long and slender; arms narrow, widely divergent in shape of a broad U, enlarged terminal plates somewhat quadrate, inner distal margins produced medially as long, slender, curved projections (Fig. 22).

Male. Size as for female, but general body color darker.

Posterior and undersurface of head, medial marginal area between eyes, frons and clypeus with moderately long, erect, dark hair. Antenna dark yellowish-brown, scape and pedicel darker; with short, fine, and some stouter, dark hair; second segment largest, bead-like; flagellum about three times as long as scape and pedicel. Palpus yellowish-brown, segment 3 and dorsal surface of 4 dark brown; with dark hair.

Pronotum and prescutum faintly lighter than scutum; sparsely covered with pale, yellow hair. Scutum dark orangish-brown, central region tinged with gray, lateral margins shining; sparsely covered with short, recumbent, yellow hair, that is more dense, longer, erect, and more pale on margins and on posterior regions; two faint, narrow, vittae visible in alcohol material. Scutellum dark yellowish-brown, but lighter than scutum, with long, erect, yellow hair. Post-scutellum dark, bare, shining. Pleuron concolorous with scutum, except for pleural membrane which is lighter and tinged with gray; pleural tuft pale. Wing veins yellowish-brown; hair on stem vein yellow, that on base of costa having pale tips and dark bases; subcosta bare dorsally except for a few hairs at tip, a single row of hairs ventrally. Fringe of calypter and alar lobe pale. Halter brownish. Legs as for female, except covered with mixture of long, yellow and brownish-yellow hair; hind basitarsus about four times as long as broad; second hind tarsal segment about 2.5 times as long as broad.

Abdominal tergites broad, dark brown, with short brownish hair; sternites sclerotized, dark brown, with longer, brown hair; anterolateral region of abdomen lighter grayish-brown; basal scale dark brown, with fringe of long, fine brown hair. Basistyle large, conic-quadrate, greatest width equal to greatest length, slightly less than twice the length of dististyle, moderately setose. Dististyle short, broad basally, tapering from about one-half its length to apex which is obliquely truncate, and possesses two terminal spines, the inner apical spine larger; lightly setose (Fig. 25). Ventral plate broad, with a thick, broad, triangular-shaped, downcurving lip; basal arms short, broad, and bluntly pointed; ventral margin of ventral plate arcuate (Figs. 26, 27). Paramer a slender, sclerotized bar that extends from the tip of the basal arm of the ventral plate to the posterior basal margin of the basistyle; this bears a single, stout, tooth-like spine on the dorsal surface at about one-half its length, and enlarges plate-like where it attaches to the basistyle. The median sclerite is short, broad, and Y-shaped, the arms are scarcely produced.

Pupa. Length, 2.5 mm.; empty pupal skins measure up to 5.0 mm. Respiratory organ, 1.5-2.0 mm. long, as long as or slightly longer than dorsum of head and thorax; with 12 filaments that arise from three widely divergent trunks that in turn arise from a short petiole (Fig. 28). Each of the three trunks bear four filaments branching as follows: the dorsal trunk with an inner, single filament, and an outer branch with three filaments; the lateral and ventral trunks each give rise to two petiolate pair of filaments, but the branching of both these trunks variable in their distance from the base. Head and thorax nearly smooth; three to five short, fine, thoracic trichomes on each side. Tergite 1 with a few, fine, scattered setae; 2 with a row of about eight fine setae on posterior margin; 3-9 with a row of small, fine, spines on anterior margin and with a few scattered fine setae; 3 and 4 with eight rather small hooks on posterior margin, these hooks smaller than those of other species of *Prosimulium* examined. Terminal spines short, arising from somewhat swollen bases, divergent apically and directed slightly anteriorly; each with a short seta at base in back. Sternite 4 with two small hooks that are somewhat laterally placed; 5-7 with four larger hooks, those of 5 ventral, and those of 6 and 7 widely separated; 8 and 9 bare except for scattered setae. Cocoon a loosely-woven sock, covering little more than abdomen of pupa.

Larva. Mature specimens 6.0-6.5 mm. long. Head capsule medium to dark orangish-brown. Frontoclypeal plate with one large dark anteromedial spot, a smaller central medial spot, a posteromedial spot, and an anterolateral and a medio-

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lateral dark spot on each side, all situated within a slightly darkened, inverted U-shaped area that extends from posterior margin of head capsule to about the level of the posterior dorsal arm of the mandibular phragma; often the head spot pattern is obscure; just anterior to the head spots on each side, is a small light spot from which a single seta projects; another, but larger light spot with one or two setae, occurs on each side just anterior and mesad of base of antennae. Epicranial plate with a dark, posterior dorsal head spot on each side; eye spots small, set in a small, pale yellow circular area, one or two pale spots occur immediately below eyes. Throat cleft V-shaped to U-shaped, widened posteriorly and tapering to a narrow, rounded apex, extends anteriorly slightly less than one-half the distance to the base of submentum (Fig. 31). Subesophageal ganglion white. Last lateral teeth of submentum longer than others; next to last lateral teeth slightly longer than median tooth; inner lateral teeth about equal in length to the median tooth; median tooth broad, secondary projections basal and short (Fig. 29); lateral margins of submentum with two or three conspicuous serrations; one long and one or two short epicranial setae on each side. Distance from apex of outermost tooth of submentum to base of anteriormost epicranial seta on same side three-fourths to five-sixths the distance between apex of outermost teeth. Mandibular phragma extending almost to lateral edge of submentum. Mandible with small teeth having relative lengths of about 5-2-10 from distalmost basad, middle tooth often difficult to see, the large basal tooth was duplicated in one specimen so that there were four teeth; following these are seven to 10 bristle-like teeth; the inner subapical margin (Fig. 30) has 15 to 20 elongate, slender teeth, the apical tooth longest and broadest. Maxillary palp dark except for apical one-third; length about 2.5 times the width at base; with scattered, small setae. Relative lengths of antennal segments, from base to apex, 4-8-9-1. Cephalic fan with about 25 rays. Pupal respiratory histoblasts with 12 filaments arising from three main, divergent trunks, four filaments on each trunk.

Abdomen of preserved specimens a light grayish-brown, with light intersegmental lines. Ventral tubercles absent. Anal gill of three simple lobes, the two lateral lobes long and curved outwards, the medial one shorter and straight. Anal cross-piece moderately sclerotized, area between arms less so; dorsal arms curved anteriorly and about twice as long as ventral arms. Anal hooks about eight per row, in 65 to 70 rows.

Holotype. Female (reared) (head and genitalia mounted on slides); small stream crossing highway 89-287, seven miles north of Leeks Lodge, Teton County, Wyoming, June 16, 1958, emerged June 20, 1958, G. R. DeFoliart, deposited in U.S. National Museum.

Allotype. Male (reared); same data as for holotype except emerged June 19, 1958.

Paratypes. One pupa, mature larvae, same data as for types; eight pupal skins, mature larvae, June 27, 1957, otherwise same data as for types; mature larvae, small stream near Camp Cloud Rim, Wasatch County, Utah, June 17, 1947, L. T. Neilson. Paratypes are deposited in the collection at the U.S. National Museum, University of Utah, University of Wyoming, University of Wisconsin, and the Canadian National Collection.

This species is named in honor of Mr. Guy Shewell, of the Entomology Research Institute, Research Branch, Canada Department of Agriculture, Ottawa, Ontario, who has done much to further the knowledge of the systematics of the northern black-fly fauna.
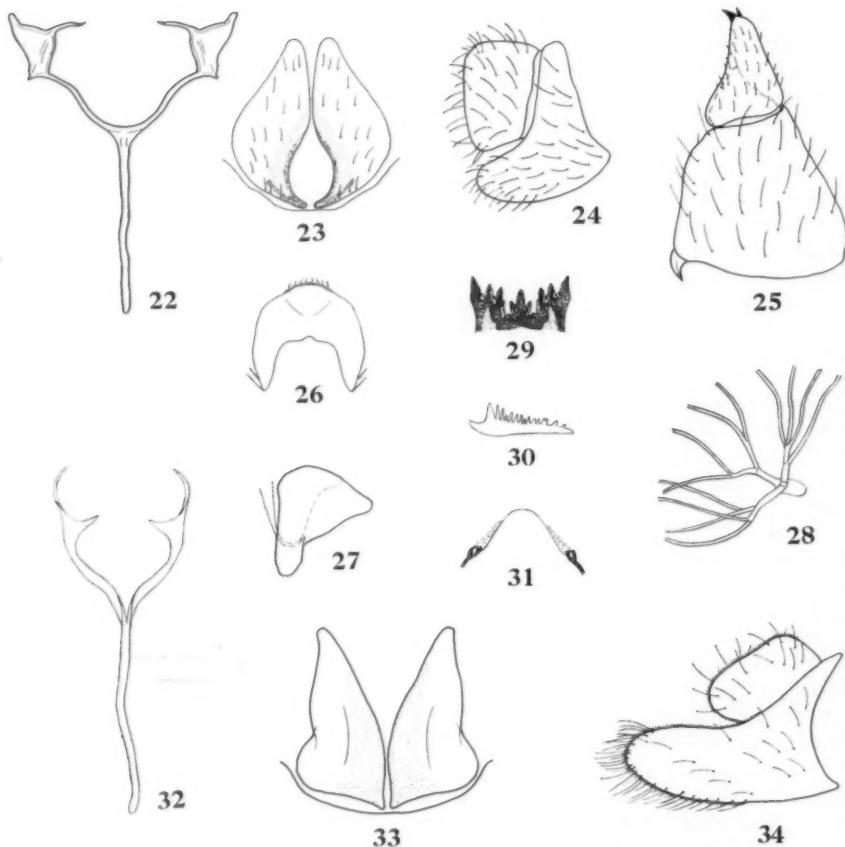
Figs. 22-31. *Prosimulium shewelli*, n.sp. Figs. 22-24, female. 22, genital rod; 23, ovipositor; 24, right anal lobe and cercus. Figs. 25-27, male. 25, right basistyle and dististyle, outer surfaces; 26, ventral plate, ventral; 27, ventral plate, lateral. Fig. 28, right respiratory organ of pupa, inner surface. Figs. 29-31, mature larva. 29, submental teeth; 30, subapical ridge of mandible; 31, throat cleft.

Figs. 32-34. *Prosimulium longilobum*, n.sp. female. 32, genital rod; 33, ovipositor; 34, right anal lobe and cercus.

Comparison With Related Species

Adults of both sexes of *P. shewelli* are easily distinguished from other species of *Prosimulium* on the basis of the genitalia. The pupal respiratory organ most closely resembles that of *P. frohnei* and *P. saltus* but can be distinguished by its pattern of branching with 12 filaments; *P. frohnei* and *P. saltus* have 12 to 14 and 12 to 16 filaments respectively. The larval throat cleft of *P. shewelli* is similar to that of *P. pleurale* and *P. travisi* but the larvae can be distinguished on the basis of the submental teeth.

Prosimulium longilobum, new species

Female. General color a shining, dark brown. Length: body, 2.5 mm.; wing, 3.2 mm.

Head dark brown, covered with moderately long, pale yellowish hair, with a row of stout, erect, dark hair at posterior and lateral margins of eyes; eyes large, extending to top of vertex. Frons shining, broad, strongly divergent above, at apex of eyes slightly more than twice as wide as at narrowest point; covered with moderately long, semi-erect, pale yellowish hair. Clypeus slightly longer than wide, with moderately long, semi-erect, pale hair. Antenna 11-segmented, shining, dark yellowish-brown, basal two segments slightly lighter; covered with short, proclinate, pale hair; second and third segments about equal in size, flagellum about three times as long as scape and pedicel. Palpus brown, third segment darker than antenna, others lighter; with moderately long, mostly pale hair; sensory vesicle of third segment bulbous, less than one-third the length of segment, and situated in proximal portion of segment; tube leading to outside short and slender, arises dorsally from distal end of vesicle. Mandible with about 42 serrations; maxilla with retrorse teeth (number not determined due to poor condition of maxilla). Median space of buccopharyngeal apparatus of a shallow U-shape; dorsolateral arms long, slender, heavily sclerotized, somewhat convergent apically.

Thorax dark brown, sub-shining; pronotum and prescutum slightly lighter, yellowed on lateral and medial edges, with moderately long, erect, pale yellowish hair. Scutum covered with short, recumbent, pale hair that is longer and more erect on lateral and posterior margins. Scutellum brownish-yellow, lighter than scutum, with long, erect, pale yellow hair. Postscutellum bare, shining brown. Pleuron slightly lighter than scutum; pleural membrane yellowish-white; pleural tuft elongate, of long, fine, pale yellowish hair. Wing veins yellowish, nearly transparent; hair on stem vein, base of costa, and underside of subcosta with pale hair. Fringe of calypter and alar lobe pale yellow. Halter yellowish-white, with fringe of short, pale hair. Legs long, brownish yellow, ends of segments and tarsi darkened; covered with long, pale yellowish hair, hair on tarsi short; hind basitarsus about six times as long as greatest width; second hind tarsal segment about four times as long as greatest width; claws simple.

Abdomen infuscate; tergal plates sclerotized, shining, 3-6 reduced in size, moderately covered with short, pale hair; rest of abdomen with dense, moderately long, pale yellow hair; terminal segments sub-shining; 8th sternite broad, heavily sclerotized. Basal scale dark, shining, with fringe of long, fine, pale hair. Anal lobe narrow dorsally, widening ventrally, produced posteriorly so as to extend beyond the posterior margin of the cercus a distance about equal to the length of the cercus itself; moderately setose on posterior and ventral margins, lightly setose elsewhere. Cercus about twice as wide as long, produced into a short, broadly rounded tip at posteroventral margin, evenly setose (Fig. 34). Ovipositor flaps broad basally, tapering to a narrow, rounded apex, inner margin heavily sclerotized; lightly setose, flaps extending nearly to tip of anal lobe and divergent distally when flattened (Fig. 33). Genital rod laterally compressed, long and sinuous; arms slightly wider than rod, diverging to form a narrow Y and twisting so as to appear flattened dorsoventrally, expanded posteriorly into somewhat triangular or C-shaped plates (Fig. 32).

Holotype. Female (mounted on two slides); Mirror Lake, Duchesne County, Utah, elevation 10,050 feet, July 26, 1952, L. T. Neilson, deposited in the collection of the U.S. National Museum.

Paratype. One female, same data as type; deposited in the collection of the University of Utah.

Male, pupa and larva unknown.

Comparison With Related Species

Prosimulium longilobum is readily distinguished from other western *Prosimulium* species by its small size, shining brown color, and distinctive genitalia. The species bears a close resemblance to *Cnephia (S.) mutata* (Malloch) in both size and color. The two females of *Prosimulium longilobum* collected were flying about humans in association with females of *Cnephia mutata* and were not distinguished from them until a study of *C. mutata* was begun.

Summary

Four new species of *Prosimulium* from western United States are described and figured. The new species are *P. daviesi*, *P. uinta*, *P. shewelli* and *P. longilobum*. The four species are compared with other closely related species, and notes on their biology are provided where such data were available.

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Effects of Changing the Phosphorus Content of the Food Plant on the Migratory Grasshopper, *Melanoplus bilituratus* (Walker) (Orthoptera: Acrididae)[1]

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Introduction

It has been demonstrated that changes in the composition of a plant influence the insects that feed upon the plant (Lipke and Fraenkel, 1956). The quantitative composition of plants can be changed by the use of fertilizers (Mulder, 1950; Rennie, 1956), and populations of insects feeding on the plants may increase or decrease (Daniels, 1957; Adkisson, 1958; Joyce, 1958). These changes in numbers of insects have been attributed to such factors as changes in nitrogen, protein, and carbohydrate content (Evans, 1938; Fritzsche *et al.*, 1957) or various mineral constituents (Creighton, 1938).

It is of interest to know to what extremes these changes in plant composition can be forced and what the resultant effect is on an insect feeding on such plants. A previous paper (Smith and Northcott, 1951) dealt with changes in nitrogen content of wheat and their effect on the migratory grasshopper, *Melanoplus bilituratus* (Walker). This paper deals with the effect of changing the phosphorus content of wheat on this grasshopper.

Methods

Renown wheat was grown in a greenhouse in vermiculite to which nutrient solution was automatically applied (Smith, 1959). To produce wheat differing in phosphorus content the wheat was grown in a low- and a high-phosphorus nutrient solution. These solutions were constituted as follows:—

	Low phosphorus	High phosphorus
$MgSO_4$	2 millimolar	2 millimolar
$Ca(NO_3)_2$	5 "	2 "
KNO_3	6 "	–
KH_2PO_4	–	6 "
$CaCl_2$	–	3 "
$NH_4H_2PO_4$	–	4 "

To each litre of these solutions was added one millilitre of the following micronutrient stock solution:—

H_3BO_3	2.86 gm./1.	
$MnSO_4.4H_2O$	2.15	"
$ZnSO_4.7H_2O$	0.22	"
$CuSO_4.5H_2O$	0.08	"
$H_2MoO_4.H_2O$	0.02	"

Ferrous sulfate solution (0.5 per cent) was applied to the surface of the growing medium about once a week at the rate of one millilitre per litre of nutrient solution. The nutrient solutions were replaced every two weeks.

[1]Contribution from the Entomology Section.

The grasshoppers were hatched in the laboratory from field-collected eggs and fed on wheat that had been grown for about four weeks on one or other of the two solutions. The first lot of 100 insects on each treatment was reared in two-quart jars, 10 per jar. An inch of soil was placed in each jar and the top was covered with fine-mesh screen. As there was considerable variation in time of development among individuals a second lot of 100 insects on each treatment was reared in individual cages like those previously described (Smith, 1959).

The grasshoppers reared in jars were fed twice daily on wheat clippings. In the individual cages the food remained fresh for some time and was replenished only every second or third day for small nymphs and daily for larger nymphs and adults.

As the grasshoppers became adult all those on one treatment were placed in a large cage containing trays of soil in which they could lay eggs. They were maintained in these cages and fed twice daily until they died.

The grasshoppers were reared in a room where the temperature was maintained at $30 \pm 1°C$. and the relative humidity at 50 ± 2 per cent.

Plant samples for analysis were taken periodically during the course of the rearing. Extra grasshoppers were reared under the same experimental conditions to provide material for analysis and were starved for 24 hours before killing. All materials were dried *in vacuo* at 100°C. for 48 hours. Duplicate phosphorus determinations were made on each plant sample and each insect by the colorimetric method of Shelton and Harper (1941).

Results

Survival to the adult stage was the same in both types of cage and was nearly three times as great on the low- as on the high-phosphorus treatment (Table I). Survival declined rapidly and steadily for the first two weeks to 50

TABLE I.

Survival and duration of nymphal period of grasshoppers fed on wheat with different phosphorus contents.

Food	Cage	Initial number of insects	Number surviving to adult	Duration of nymphal period	
				Days	Standard deviation
Low-P wheat......	Jars	100	29		
	Individual	98	29	32.2	2.7
High-P wheat.....	Jars	100	11		
	Individual	100	11	42.8	4.2

and 30 per cent on the low- and the high-phosphorus treatments, respectively, then continued to decrease at a much slower rate until the adult stage was reached. Differences in survival were greatest in the first-instar nymphs, 73 per cent of which survived on the low-phosphorus treatment and only 54 per cent on the high-.

Development was noticeably more rapid on low-phosphorus wheat; when 70 per cent of the insects were in the fourth instar on low-phosphorus wheat only 25 per cent were in that instar on high-phosphorus. The total nymphal period was 10 days longer on high-phosphorus wheat. An extra instar between the

usual third and fourth instars appeared in 63 per cent of the survivors on high-phosphorus wheat and in 59 per cent of those on low-.

Both sexes survived equally well on both diets. Thirty-one males and 27 females survived on low-phosphorus wheat and 10 males and 12 females on high-. The 27 females on low-phosphorus wheat laid 33 egg pods. No eggs were laid by the surviving females on high-phosphorus wheat.

The percentages of phosphorus and various other elements in wheat from the two treatments are shown in Table II. The only evident difference between

TABLE II
Analysis of wheat grown on low- and high-phosphorus solutions
(percentage dry weight)

Treatment	Phosphorus		P*	N*	K*	Mg*	Ca*
	Mean	Range					
Low P...............	0.17	0.04–0.23	0.25	4.15	6.11	0.35	0.38
High P..............	1.86	1.36–2.28	1.81	4.42	5.83	0.39	0.49

*Macro determinations on bulked samples made by the Chemistry Division, Department of Agriculture, Ottawa.

the wheats was in the phosphorus content. The phosphorus content of the grasshoppers as a percentage of dry weight was:—

	Mean	Range
Fed on low P wheat.............	0.57	0.42-0.85
Fed on high P wheat.............	0.83	0.74–0.95

Although the range of phosphorus content reached lower levels in the grasshoppers raised on low-phosphorus wheat than in those on high-, the variation was too great for this difference to be significant.

Discussion

Wheat grown on the low-phosphorus treatment was obviously a better food for *M. bilituratus* than that grown on the high-. There was no indication whether phosphorus or some other substance whose abundance was correlated with that of phosphorus was the effective factor, but there were no marked differences between the two treatments in the amounts of any of the other elements shown in Table II. Allen and Selman (1957) have reported that *Pieris brassicae* (L.) has a small larval weight and a long development period when reared on turnip leaves grown in a phosphorus-deficient medium whereas Dahms (1947) has reported that *Blissus leucopterus* (Say) laid more eggs when reared on seedling sorghum grown in a phosphorus-deficient medium. It may be that these two investigations were conducted on ranges of phosphorus content that were on opposite sides of an optimum. Allen and Selman did not analyze their plant material, but Dahms found values for the phosphorus content of plants on a low-phosphorus treatment that were higher than those recorded for ordinary field-grown sorghum (Webster *et al.*, 1948). All his material could have been above the optimum value so that the best food would be that with the lowest phosphorus content. Rodriguez' work on *Tetranychus bimaculatus* Harvey

(1951) indicates the presence of such an optimum. Mite populations were positively correlated with the phosphorus content of tomato leaves up to a level of 0.30 per cent and negatively correlated above this. In the present work, phosphorus in the wheat grown on the low-phosphorus solution could have come only from that in the seed or from impurities in the solution. Yet the phosphorus level in this wheat was not very much lower than that commonly present in field-grown wheat. Steyn (1951) also was only partially successful in lowering the phosphorus content in lemon seedlings by using nutrient solutions. The optimum phosphorus content in wheat for *M. bilituratus* may be in the neighborhood of the lower values reported here.

The survival of 29 per cent on low-phosphorus wheat is small. The wheat in both treatments had a nitrogen content of approximately four per cent, and this may have depressed the percentage survival. In previous work (Smith and Northcott, 1951) there was only a 30 per cent survival of *M. bilituratus* reared on wheat containing four per cent total nitrogen. A survival of about 50 per cent is to be expected on 'normal' wheat (Smith, 1959). The rather high frequency of occurrence of extra instars on both treatments was another indication that the food was not fully adequate.

This and the previously mentioned work on nitrogen in wheat show that the size and fecundity of a population of grasshoppers can be considerably influenced by changes in its host plants. Although these changes may seem relatively great, the plants on all treatments appeared healthy and were able to head. This raises the interesting possibility that judicious management of fertilizer applications may directly benefit the host crop and, at the same time, by rendering it less suitable to one or more of its insect pests, actually bring about a decrease in the size of the pest insect population.

Summary

The phosphorus content of wheat was changed by the use of nutrient solutions and the wheat was used as food for the migratory grasshopper, *M. bilituratus* (Walker). Survival, rate of development, and fecundity were all greater on wheat with a low-phosphorus content (0.17 per cent dry weight) than on wheat with a high-phosphorus content (1.86 per cent dry weight).

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New Oriental Trogini (Hymenoptera: Ichneumonidae)

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Neofacydes, new genus

Type.—Neofacydes sinensis n.sp.

Flagellum.—Female flagellum moderately long, lanceolate, widened beyond the middle and strongly attenuated at the apex; basal segments of the male flagellum cylindric, at the apex however obliquely cut and overlapping, becoming gradually more distinct nodose beyond the seventh segment.

Head.—Occiput hardly emarginate, sloping down steeply behind the ocelli and eyes; cheek profile strongly narrowed with straight outline; median field of the face well defined; clypeus normal with straight apical border; frons concave; mandibles normal with small teeth.

Thorax.—Mesoscutum moderately convex, a little longer than wide; scutellum pyramidal; propodeum as in *Trogus* Panzer, the area posteromedia wide, parallel-sided, the upper border arched; areae posteroexternae with strong lateral carinae.

Legs.—Relatively long and slender.

Abdomen.—Female abdomen oxypygous, similar in appearance to a *Coelichneumon* abdomen; surface of tergites 1-5 strongly aciculated, tergites 1-5 strongly separated, sometimes with sharp lateral edges, but not bulging laterally; postpetiolus with aciculate median field; gastrocoeli deep, transverse.

Distribution

Evidently confined to the oriental tropics; replaced in the Neotropics by the genus *Macrojoppa*.

Neofacydes sinensis, new species

Facydes purpureomaculatus Heinrich (nec Cameron), 1931, Zeitschr.Angew.-Entom., 18: 398, ♀ ♂.

Facydes purpureomaculatus Mell, loc. cit., pp. 372, 377, 379, 386, 388, 390, 394, 395.   (Biological notes).

Holotype.— ♀ , Formosa, Taiheiran, 9.˙7. 1934, leg. L. Gressitt, in Collection H. Townes.

Female and male

Very similar in color to *Facydes purpureomaculatus* Cameron, except that the apical tergites lack the metallic purplish tint characteristic for Cameron's species.

Fulvous-ferruginous; tergites 4-7 black; apex of tibiae III and the tarsi III black; flagellum black, without annulus; yellowish are sides of the face and indistinctly the orbits; length 15 mm.

Flagellum.—Distinctly widened beyond the middle, strongly attenuated at the apex, with 36-37 segments, the widest about twice wider than long, the eleventh square.   Black, scape ferruginous.

Abdomen.—Not widened, rather slender, the second tergite not wider than long, the third about twice wider than long; tergites laterally rounded, without indication of the formation of a lateral edge.

Hosts

Known only of the type of the genus: the sphingid *Oxyambulyx sericipennis* Btl.

Remark

The genus is related to *Trogus* Panzer, differing from the latter in the female sex mainly in the oxypygous abdomen and the lanceolate flagellum, also in the laterally not bulging tergites.   The male flagellum differs from *Trogus* in that its basal segments are not nodose.

More closely allied to the Neotropical genus *Macrojoppa* Kriechbaumer. Both genera agree in the morphology of the oxypygous abdomen.   *Neofacydes* differs from *Macrojoppa* in the pyramidal scutellum and in the areolation of the declivous part of the propodeum.

Neofacydes marlisae, new species

Holotype.— ♀ , North East Burma, Maymyo, 800 m. Akadamja Nauk, Instytut Zoologiczny, Warsaw; collection Gerd Heinrich.

Distribution

North Burma (Chin Hills) and North East Burma (Shan Plateau), 800-1400 m.

Female

Smaller and more slender than *nigrolineata* Cameron; tricolored; head and abdomen black with extended white pattern, thorax blood-red; wings strongly infuscated except basal part; flagellum black; length 11-15 mm.

Flagellum.—Lanceolate, moderately long and widened beyond the middle, strongly attenuated at the apex, with 36 segments, the widest not quite twice as wide as long, the eleventh square.   Black, scape below and at the base white.

Color.—Black; thorax red, reddish white below; white are base of the mandibles, cheeks, face entirely or laterally, apical margin of clypeus, orbits around the eye (more or less narrowly interrupted at the vertex), scape below, legs I and II below, narrow base of tibiae I and II, basal half of tibiae III, lateral fields of the postpetiolus and third tergite except base. Wings purplish-gray infuscated, becoming gradually clear toward the base.

Male

Face and clypeus more extended white colored than in the female, usually entirely white or sometimes with a small black median mark on the clypeus,

rarely also the middle of the face infuscated; white orbits interrupted broadly at the temples.

Remark

Dedicated to Mrs. Marlis Wolff, who in 1937 collected this and many other rare species in Burma.

Neofacydes townesi, new species

Holotype.— ♀ , Philippines, Los Banos, Laguna Provinces, Philippines, 3.X.1953, leg. Townes Family, in collection H. Townes.

Female

An aberrant, striking species, distinguished by abbreviation of mesoscutum, scutellum, propodeum and abdomen and by presence of an infuscated cloud in the anterior part of the apex of the forewings; tergites 2-5 black, the second with broad, whitish, the third to fifth with narrow, brownish apical bands; tergites 6 and 7 entirely yellowish-brown; length 14 mm.

Flagellum.—Bristleshaped, unusually slender, with 38 segments, distinctly widened beyond the middle, tapering apically into an extremely long and fine tip, the basal segments strongly elongate. Blackish above, scape and the nine basal segments ventrally yellowish.

Head.—Mainly yellowish; mandibles black; middle of face and clypeus somewhat infuscated; the following are blackish: middle of frons broadly, ocellar region, occipital region up to the vertex (except a yellowish central mark behind the ocelli) and the apex of cheeks.

Thorax.—Mesoscutum short, of equal longitudinal and transversal diameter, very densely rugously punctured; scutellum abbreviated, relatively low, pyramidal, with a very wide, plain apical slope; propodeum abbreviated with unusually short anterior slope. Black, variegated with yellowish white and obscure reddish. The following are yellowish white: collare, upper and lower border of pronotum, median crossband of scutellum, prosternum, irregular pattern of mesosternum and lower half of mesopleura, prepectus in part and anterior border of area posteromedia. The following are obscure reddish: indistinct longitudinal bands of the three lobes of mesoscutum, speculum of mesopleura, sutures of propodeum and irregular patches of mesopleura and mesosternum.

Legs.—Slender, blackish brown; the following are yellowish: femora and tibiae I and II internally, tibiae III at the base and ventrally in the basal half, all metatarsi ventrally, coxae I and II and coxae III ventrally in part.

Abdomen.—Relatively short and wide, second tergite a little wider than long, the third more than three times as wide as long; petiolus pale yellowish, postpetiolus obscure brownish, tergites 2-5 black, the second with broad, white, the third to fifth with narrow obscure ferruginous apical band; tergites 6 and 7 entirely yellowish brown.

Pedinojoppa, new genus

Type.—*Pedinopelte orientalis* Szepligeti.

Szepligeti's species can not be included in the Neotropical genus *Pedinopelte* Kriechbaumer because it differs from the latter by an important character: the vertex is strongly elevated behind the ocelli as in the Oriental genus *Holcojoppa* Cameron. Although more closely related to *Holcojoppa* than to *Pedinopelte*, the species *orientalis* can not be placed in *Holcojoppa* either on account of its flat scutellum.

The distribution of *Pedinojoppa*, new genus, seems to be restricted to the Indo-Malayan region, where it was recorded from Celebes (holotype), Java (Zool.Mus. Berlin) and Sumatra (Col. G. Heinrich in Warsaw).

The Spider Population of a Stand of Oak (*Quercus robur* L.) in Wytham Wood, Berks., England[1]

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In an assessment of spider predation on insects, an arbitrarily delimited woodland community was examined to determine the species of spiders present and their abundance and distribution therein. Periodic samples were taken from September, 1954, to September, 1956.

The Study Area

The study area, on the northern slope of Wytham Wood, Berkshire, consists of about 0.25 hectares (0.62 acres) of heavy clay soil supporting 21 large-crowned oaks (*Quercus robur* L.) about 18 metres (60 feet) in height. The plot is inclined to the north-east with a mean slope of about 10 per cent. *Q. robur* is the only tree species in the study area, but a mixed deciduous forest surrounds the stand. Before 1947 the ground beneath the canopy was overgrown with hawthorn (*Crataegus oxycanthoides* Thuil.) and bramble (*Rubus* sp.). In 1947 the hawthorn and bramble were removed, but, in spite of periodic recleaning, small clumps of these plants persist. Two dense stands of willow-herb (*Chamaenerion angustifolium* (L.) Scop.) occupy unshaded parts of the area. The remainder of the plot is covered by a mixture of herbaceous plants, mostly grasses (Fig. 1).

Sampling Methods

The community was divided into four of the seven layers of habitat structure described by Elton and Miller (1954): the ground zone, the field layer, the low canopy, and the high canopy. As different sampling procedures were required for each stratum the results of each sample were converted to a common unit, viz., the number of spiders contained in a column standing on one square metre of soil surface and extending upward to the mean height of the tree tops. Crude sampling methods were used, and it is probable that errors inherent in the sampling methods exceed the calculated standard errors as derived from sample variation. All samples were taken between 10.30 a.m. and 4.30 p.m., G.M.T.

The Ground Zone

This layer consists of the soil surface, the organic litter, inorganic debris, and all plants up to a height of 15 centimetres (six inches).

Samples were taken with a metal box 50 centimetres square and 16 centimetres in depth with a removable one-quarter-inch mesh screen at the top and a sliding bottom, one edge of which was sharpened. With top and bottom removed the box was pressed into the organic layer to the level of mineral soil. Protruding plants were carefully cut off level with the top of the box, i.e., at a height of 15 centimetres, and the wire-mesh top was fitted. The metal bottom was forced into place between the soil surface and the organic layer, the sharpened edge severing the roots of plants. The closed box was lifted, inverted over a cotton sheet and shaken violently. Most of the animals present tumbled onto the sheet and were collected. The residual material was placed in a polythene bag and later extracted in a Tullgren funnel. Five more-or-less randomly distributed samples were taken once a month from April to December.

STUDY PLOT
WYTHAM GREAT WOOD, BERKS.

HIGH CANOPY OF OAK
LOW CANOPY OF OAK
CHAMAENERION
ANGUSTIFOLIUM L.
BRAMBLE & WOODY SHRUBS

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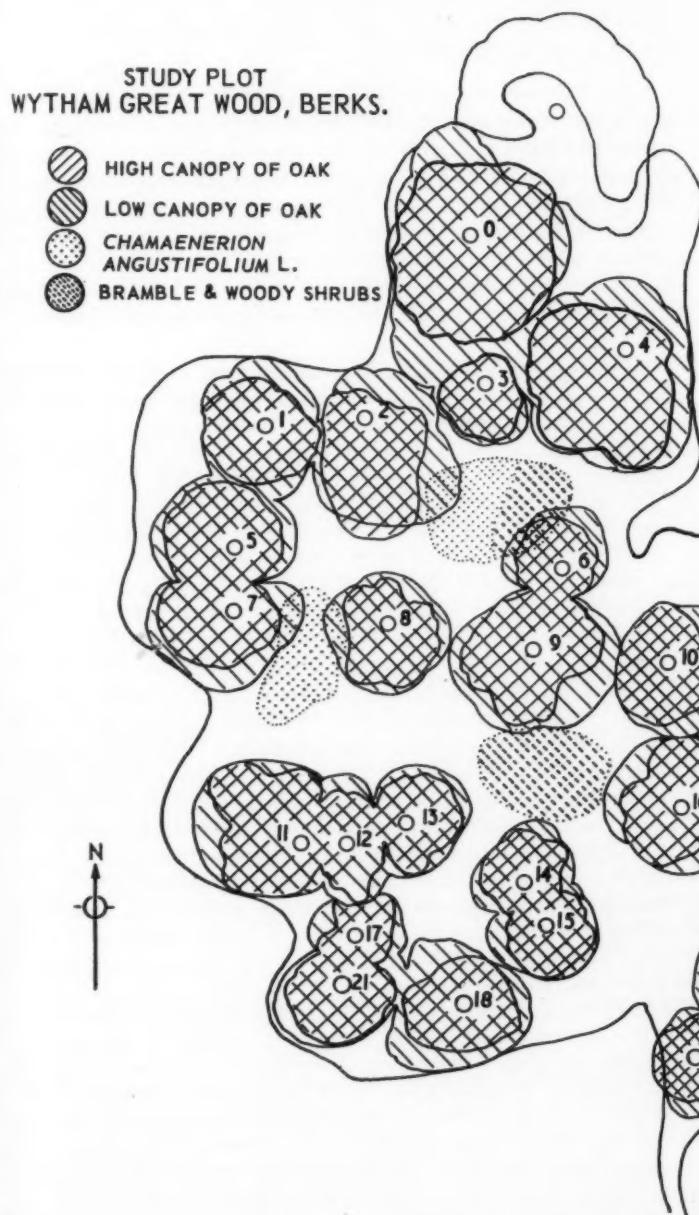
Fig. 1. Study plot, a stand of 21 oak trees, Wytham Great Wood, Berkshire, England.
Plot is inclined to north-east with mean slope about 10 per cent.

The method was presumed to provide a sample of all the spiders in a column 0.25 square metres in area and 15 centimetres in height. To convert the mean number per sample to the mean number per square-metre column of ground zone, the mean per sample was multiplied by four.

The Field Layer

This stratum consists of the vegetation higher than the ground zone up to a height of 1.8 metres (six feet).

The layer was sampled with a Britten sweep net 30.5 centimetres (12 inches) in diameter. Two marking cords 30 feet long were laid out parallel to each other 1.4 metres apart. Each sample consisted of 10 consecutive sweeps between these cords, five sweeps to the right and five to the left. Care was taken to keep the net completely submerged in the foliage for the full arc of each sweep. Ten samples distributed more-or-less at random throughout the area were taken each week from April to December.

The volume of foliage sampled with each sweep was equivalent to the volume of a cylinder with a 30.5 centimetre diameter and 140 centimetres in length, or 0.10 cubic metres. Ten sweeps, or one sample, thus provided an estimate of the spider population in one cubic metre of field layer vegetation. The mean height of vegetation on a given sampling day, minus the height of the ground zone (15 centimetres), is proportional to the volume of vegetation in an average square-metre column of field layer. (Volume = height in metres x 1 square metre). Thus, the mean number of spiders per cubic metre as derived from the sample, multiplied by the mean height of the vegetation minus 15 centimetres on the day the sample was taken, provides an estimate of the number of spiders in an average one-square-metre column of field-layer vegetation.

The deficiencies of sweeping as a sampling method are discussed by several authors (Carpenter and Ford 1936, De Long 1932, Hughs 1955, Johnson, Southwood, and Entwhistle 1957). The efficiency of the method varies from time to time, depending on day-to-day variables such as weather. However, sweeping provides a simple and quick method of obtaining a rough estimate of the number of arthropods active at the time samples are taken, which fulfils the purposes of this study. Some of the animals present are probably missed by the sweep net, but, as no method was devised to check the magnitude of this error, the number of spiders captured in the samples are taken to represent all of the spiders on the foliage swept. These samples, therefore, probably underestimate the numbers of spiders in the field layer.

The Low Canopy

This stratum consists of the tree canopy up to a height of 7.5 metres (25 feet).

A beating tray one metre square was held close beneath the low canopy so that foliage liberally overlapped all sides for at least two metres above the tray. One hundred taps with a beating stick were distributed throughout the column of foliage above the tray for a vertical distance of two metres. Thus about two cubic metres of foliage were sampled. Ten samples, distributed more or less at random throughout the area, were taken weekly from April to December.

The volume of foliage in a one-square-metre column of lower canopy within a tree crown is proportional to the height of the foliage in the column (Volume = height in metres x 1 square metre). The height of foliage is the difference between the heights of the lower and upper margins of foliage in the layer. The

mean height of the lower margin was estimated to be 1.9 ± 0.4 metres by averaging the distance from the ground to the lowest tree branch midway between the tree stem and the branch tip at the four cardinal points of the compass for each of the 21 trees in the plot.   The upper edge of the low canopy was defined as 7.5 metres.   Accepting 1.9 metres as the best estimate of the height of the lower margin, the mean height of foliage in the stratum is $7.5 - 1.9 = 5.6$ metres. But only 63.2 per cent of the total plot area was covered by tree canopy, estimated by placing a squared grid over a scale map of the area and counting the squares occupied by canopy (Fig. 1).

As the volume of foliage sampled was two cubic metres, the mean height of foliage in the layer was 5.6 metres, and 63.2 per cent of the ground area was covered by canopy, the estimated number of spiders in an average square metre column of low canopy is:

$$\text{mean number per sample} \times \frac{5.6 \times 1 \text{ metre}^2 \times .632}{2} = \text{mean number per sample} \times 1.77$$

This method does not take into account tree growth or increasing canopy coverage of the area.

The High Canopy

This stratum consists of the tree canopy above 7.5 metres (25 feet).

This layer was also sampled with a beating tray.   The method required climbing high into the crown and balancing precariously on slender branches to reach peripheral foliage.   Five samples of two cubic metres of foliage were taken once a month from April to December.

The mean height of the upper margin of foliage was estimated by averaging the heights of all trees in the plot as measured by a forester's hand level.   The mean height of the trees was 18.1 ± 2.3 metres.   As the lower margin was designated as 7.5 metres the mean height of foliage in the stratum was $18.1 - 7.5 = 10.6$ metres.   Forty-two and one-half per cent of the ground area was estimated from Fig. 1 to be covered with upper canopy foliage.   The estimated number of spiders in an average square-metre column of high canopy layer is therefore:

$$\text{mean number per sample} \times \frac{10.6 \times 1 \text{ metre}^2 \times .425}{2} =$$

mean number per sample x 2.25.

Beating probably has all the deficiencies of sweeping as a sampling method. It is improbable that all of the spiders that occur on the foliage are captured.   As no adequate method was devised to check the magnitude of the error thus caused, however, it is assumed that the spiders captured by beating constitute the entire population in the sampled foliage.   This assumption probably causes the numbers of spiders in the canopy layers to be underestimated.

Treatment of Sample Collections

Counts were made of all spiders collected in the samples, and the mean numbers per sample for each sample day were calculated for each layer.   These numbers were then converted to the estimated number per one-square-metre column of each stratum.   A summation of the numbers in each stratum provided an estimation of the numbers per one-metre-square column of forest.   All spiders were identified as closely as possible, adults to species and immature to higher categories, i.e., genus or family.   The spiders in each sample were then desiccated for eight weeks, and weighed.   The dry weights thus obtained were

treated similarly to the figures obtained by counts of spider numbers, and an estimate of the total biomass of spiders in a square-metre column of forest was derived.

Results and Discussion

The sampling methods used in this study do not provide a measure of the absolute numbers of spiders living within the study area. There are many parts of the environment, such as large branches and stems of trees, bark crevices, mosses and lichens, and cavities and crotches on these parts, cavities at the bases of tree stems, hollow stems of herbs, soil crevices, burrows, etc., which were not sampled at all. In fact, the samples included very few of those places into which spiders retire during their periods of inactivity. What were sampled, however, were most of the places where spiders are found during their periods of activity. The samples thus provide an estimation of the spiders which were active in the area at the times the samples were taken.

Abundance of Spiders

Fig. 2 shows the estimated abundance and biomass of active spiders per square metre of forest floor for the two-year period between September, 1954 and September, 1956. The low abundance from late autumn to early spring shown in Fig. 2 is partly due to an actual low abundance of many species during this period, and partly to a withdrawal of other species to winter shelters. Many of the common species of spiders overwinter in the egg stage and, though this is undoubtedly the stage of maximal abundance, eggs were not counted in this study. Most of the remaining species overwinter as immatures, either as early-stage juveniles or as sub-adults. During the winter the environment under the forest canopy is excessively humid, cold, and poorly lighted. Under these conditions overwintering immatures remain quiescent, although they are fully capable of movement and resume activities during any prolonged warm or sunny period in the winter (Duffy, 1956). In spring, commencing about mid-March, there is a rapid upsurge in the numbers of active spiders, to which both reactivated over-wintered immatures and newly hatched spiderlings from overwintered eggs contribute. This early spring activity is confined to the ground zone which is the first stratum to warm up. Intense activity in the field layer soon follows, but it is not until mid-April that much activity is apparent in the canopy levels. The delay in activity in the canopy is probably connected with development of foliage in the crown. A peak in the numbers of active spiders is reached about mid-summer, when a sharp decline of numbers commences. This latter is due to two causes: species which overwintered as sub-adults have achieved maturity, oviposited, and have commenced to die; at the same time most of the overwintered eggs have hatched, and the dispersal of spiderlings and normal mortality have begun to exceed the number of new hatchings. This decline continues until mid-September, when numbers again rise to a second but lesser peak in October. This peak reflects the hatching of the eggs laid in midsummer. The decline in autumn reflects a retirement of immatures to winter shelters, plus mortality of the matured individuals that arose from overwintered eggs the previous spring.

This pattern of population development was consistent for the one full year and two part years sampled. If the data for the end of 1954 are placed in the corresponding position behind the data for the spring and summer of 1956, the composite curve obtained agrees remarkably well with the curve for the full 1955 data.
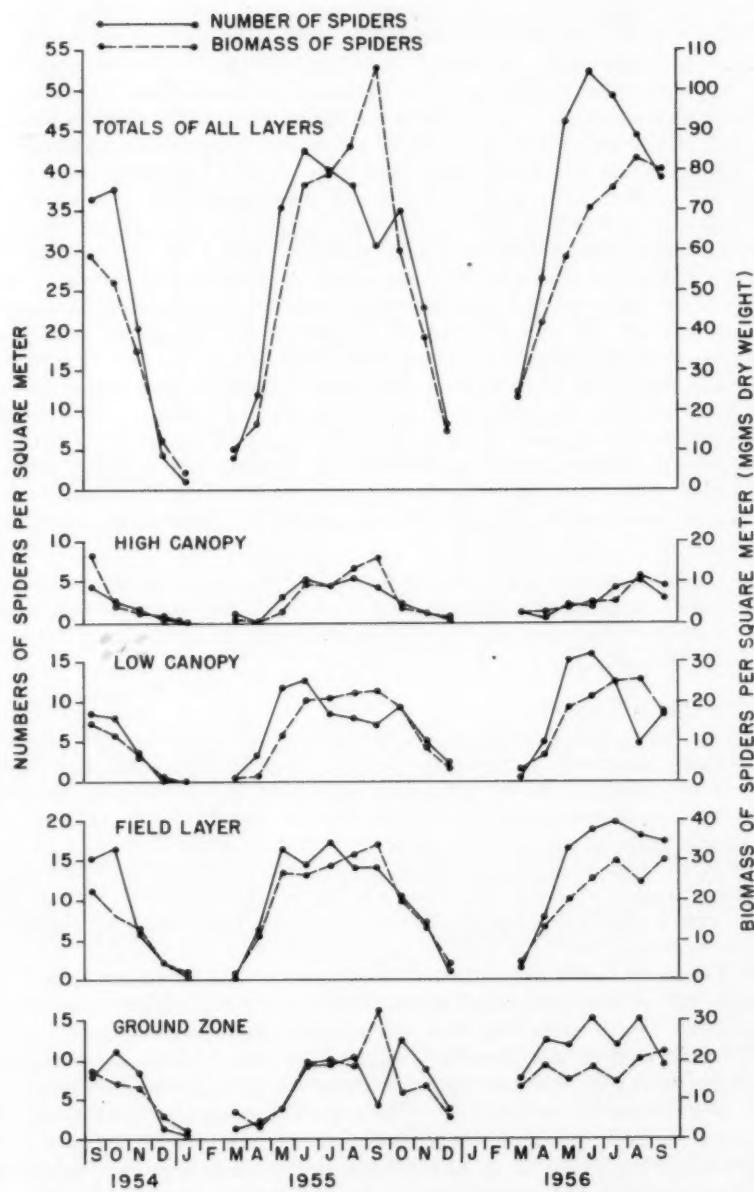
Fig. 2. Mean monthly numbers and biomasses of active spiders in each of four main structural layers and totals of all layers in oak study plot, Wytham Great Wood, Berkshire, England. All samples taken between 10.30 a.m. and 4.30 p.m., G.M.T.

Biomass of Spiders

The curves representing the estimated biomass of spiders reflect the combined effects of the abundance of the population and the sizes of individuals that make up the population. Apparently the latter of these effects predominates. There is a minor peak of biomass at the time of maximal abundance, but, whereas the abundance curve declines at this point, the biomass curve continues to rise. The peak of abundance is created largely by the hatching of overwintered eggs. The large numbers of minute spiderlings thus produced contribute only in a minor way to the total biomass. But at this time species that overwintered as immatures are beginning to reach maturity and egg-swollen females are becoming abundant. These heavy-bodied females contribute much to the first peak of biomass. Before the effects of these individuals are dissipated by mortality, rapid growth of the early spring generation makes itself felt, and biomass continues to rise at a reduced rate. At the end of August the increase of biomass greatly accelerates as the spring generation matures and the females become swollen with eggs. The main peak of biomass is achieved in mid-September, just at the time of minimal summer abundance. From this point the biomass curve declines sharply and persistently because of natural mortality of autumn-matured females. This decline is influenced only slightly by the October rise in the numbers of individuals. The minute hatchling spiders responsible for the late-autumn rise in numbers are too small to alter the downward trend of biomass at this time of the year.

It is interesting to note that though population numbers achieved a significantly higher peak in 1956 than in 1955 ($p = 0.5$) biomass was significantly lower in 1956. This may indicate an intensification of competition at higher population densities.

Stratification of Populations

Fig. 2 shows that throughout the summer months the spider population is about equally distributed between the ground zone, the field layer, and the two layers of the canopy. As the strata vary greatly in depth, however, this figure provides an inaccurate picture of the densities of populations in each stratum. The ground zone is only 15 centimetres in depth, the habitable part of the field zone (i.e., the part occupied by vegetation) varies over the seasons between 35 and 75 centimetres in depth, the lower canopy is 560 centimetres, and the high canopy 1060 centimetres in depth. The low canopy, however, covers only 63.2 per cent of the ground area, and the high canopy only 42.5 per cent. It is apparent that open spaces between tree crowns are uninhabitable by spiders, and the population is necessarily confined to those parts of the environment actually occupied by tree crowns. An effective measure of population density is one which would estimate the number of spiders per unit volume of environment. This is shown in Fig. 3, which represents the number of spiders per cubic metre of the habitable part of each stratum. From this figure it is clear that the maximal density of the spider population is concentrated near the ground, and populations become increasingly diffuse as height from the ground increases. In fact the density of spiders in the ground zone is always more than twice that in the field layer, which in turn is more than four times the density in the canopy layers.

The spring populations of spiders in the higher strata arise from two sources: those that overwintered in these layers; and those that overwintered in the ground zone and migrated upward in the spring, thus escaping the intense competition
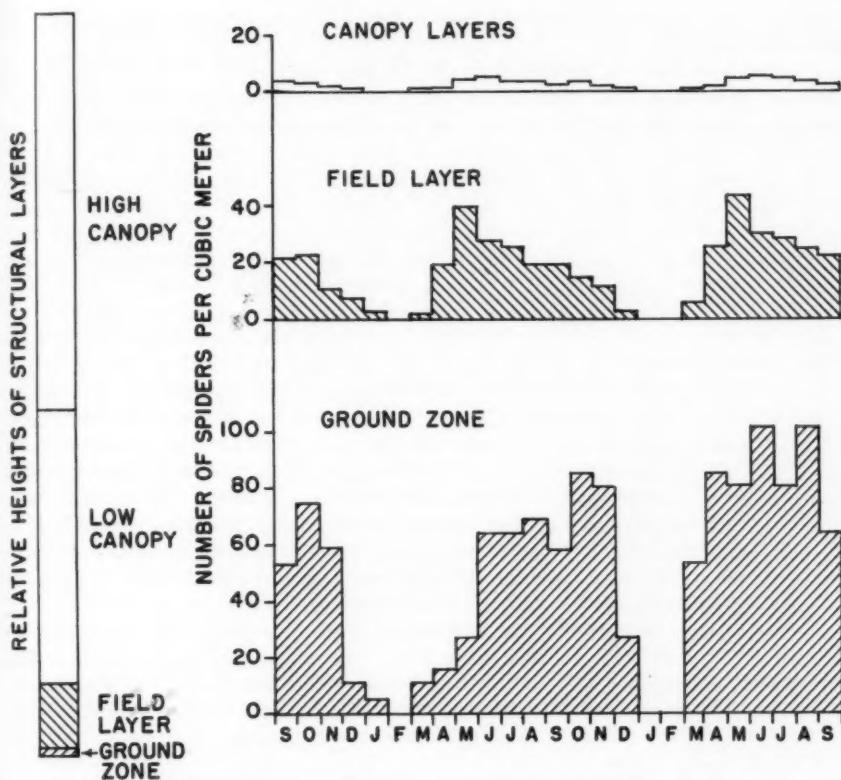
Fig. 3. Relative heights of four main structural layers of oak study plot, Wytham Great Wood, Berkshire, England, and densities of spiders (number per cubic metre) in ground zone, field layer, and canopy layers (mean of high and low canopy—Fig. 2).

that prevails in the high-density populations of the ground zone. These latter spiders consist mainly of web-builders that require three-dimensional space in which to suspend their webs. The maximal density of these spiders is limited by sufficient unobstructed space in which to suspend their webs.

The upward emigration of spiders delays the growth of high population densities in the ground zone until the emigration is completed about the end of May. From this time onward densities in the ground zone rise rapidly to high levels because of the hatching of eggs of typical ground-zone species, principally Lycosids. Densities in the ground zone remain remarkably constant at a high level until early autumn when a further rise occurs. This autumn rise corresponds to a decline in the densities of higher strata, and represents a return to the ground of species from the field and canopy layers for overwintering.

Stratification of Species

There is a strong tendency for stratification of spider species in the vertical structural layers of the forest, though this tendency is much obscured by seasonal and diurnal movements. Though many species have a preferred stratum in

which they are most commonly found, they tend to overflow this and invade adjacent strata.

The field layer is the richest in species, and representatives of practically all species present in the environment were found there. The field layer constitutes the zone of demarcation between typically ground-inhabiting species and typically canopy-inhabiting species. Typical ground-inhabiting species, (e.g., *Lycosa pullata* (Cl.), *L. lugubris* (Walck.), *Ceratinella brevis* (Wider), *Gonatium rubens* (Bl.)), invade the field layer from below, but seldom reach the upper extremities of this stratum, and almost never venture above it. Typical canopy-inhabiting species, (e.g., *Clubiona brevipes* Bl., *Anyphaena accentuata* (Walck.), *Xysticus cristatus* (Cl.), *X. lanio* C.L.K., *Philodromus rufus* Walck., *Diaea dorsata* (Fabr.), *Theridion vittatum* C.L.K., *T. neglectum* Wiehle, *Meta segmentata* (L.), *Zygiella atrica* C.L.K.), invade the field layer from above but rarely venture to the ground zone, except perhaps in the autumn, or as the result of an accidental fall. In addition to these invaders, the field layer has a rich variety of resident species (e.g., *Clubiona pallidula* (Cl.), *C. lutescens* Westr., *Micrommata virescens* (Cl.), *Pisaura mirabilis* (Cl.), *Amaurobius atropos* (Walck.), *Theridion varians* Hahn., *Tetragnatha obtusa* C.L.K., *Meta merianae* (Scop.), *Cornicularia cuspidata* (Bl.), *Gongylidium rufipes* (Sund.), *Hypomma cornutum* (Bl.), *Drapetisca socialis* (Sund.), *Stemonyphantes lineatus* (L.), *Lepthyphantes minutus* (Bl.), *L. tenuis* (Bl.), *Linyphia triangularis* (Cl.), *L. peltata* Wider), which in turn invade adjacent layers. The high canopy is the poorest in species, and constitutes a marginal upward extension of the low canopy.

There are a few species which show no discernible preference for any level above the soil surface. In the study area these include *Theridion pallens* Bl., *Tetragnatha montana* Sim., *Araneus gibbosus* (Walck.), and *A. inconspicuous* (Sim.). The most abundant spider species in the area is *Theridion pallens*, which was found in large numbers in all strata above the ground.

Species Composition of Spider Populations

Spiders can be identified to species only in the adult stage. Immatures can be placed in higher categories, usually genus, with reasonable confidence but, particularly in family Linyphiidae, identification of many immatures to categories below sub-family is risky. As most of the specimens taken in these samples were immature it is not possible to give data on the abundance of each species. In the following notes, therefore, abundance of immatures will be given for the lowest practical categories; abundance of adults will be given for those species which exceed a density of 0.1 adults per square metre.

Fifteen families of spiders are represented in the samples by a total of 98 species, though some families are represented by a single species which may be rare in this environment. Except where otherwise indicated, the nomenclature used is that of Locket and Millidge (1951, 1953). In all cases figures indicating the abundance of spiders represent the estimated number per square metre.

FAMILY DYSDERIDAE
Lathys humilis (Bl.)
Lathys: immatures occasionally in field layer in late summer and autumn; greatest density about 0.1, in August. *L. humilis* adults in May and early June.

FAMILY DYSPERIDAE
Harpactea hombergi (Scop.)
Harpactea: no immatures recognized as such. As *H. hombergi* is said to inhabit

cracks and crevices, the lack of immatures may be because of inadequate sampling. Three males of *H. hombergi* in winter on the ground.

FAMILY GNAPHOSIDAE

Drassodes lapidosus cupreus (Bl.); *Scotophaeus blackwalli* (Thor.); *Zelotes latreillei* (Sim.).

Drassodes: immatures rare, found on ground from May to October. Two *D. lapidosus* females, one in August, one in September, from field layer. *Scotophaeus*: three immatures in ground zone, in summer. One *S. blackwalli* from field layer in August. *Zelotes*: immatures rare, from ground zone and field layer in summer. Two *Z. latreillei* from field layer in August.

FAMILY CLUBIONIDAE

Clubiona reclusa O.P.-C.; *C. coerulescens* L.K.; *C. pallidula* (Cl.); *C. neglecta* O.P.-C.; *C. lutescens* Westr.; *C. compta* C.L.K.; *C. brevipes* Bl.; *C. diversa* O.P.-C.; *Agroeca brunnea* (Bl.); *Zora spinimana* (Sund.).

Clubiona: immatures abundant in field layer and low canopy from early spring to late autumn; greatest density about 5.0 in July, highest density in field layer but also abundant in other strata. Adults of all species in spring and early summer. *C. pallidula*, (0.48 in June), *C. lutescens*, (0.42 in May), *C. reclusa*, (0.82 in May), mainly from the field layer, and *C. brevipes*, (0.52 in May), mainly from the low canopy, were the only species exceeding a density of 0.1 as adults. One female *C. coerulescens* from field layer in June. Adults of remaining species taken occasionally. *Agroeca*: immatures difficult to distinguish from *Clubiona*. As only three adults of *A. brunnea* were taken from the field layer in late June, the number of immatures was probably small. *Zora*: immatures rare in summer. Three adults of *Z. spinimana* taken from ground zone in November.

FAMILY ANYPHAENIDAE

Anyphaena accentuata (Walck.)

Anyphaena: *A. accentuata* is the only British representative of this family and is therefore recognizable in all stages. Abundant; equally distributed in field layer and low canopy. Greatest density of immatures 3.2 in August. Adults in April, May, and June; greatest density (0.72) in mid-May, and this density maintained until late June. But, whereas two-thirds of adult population was in the field layer in May, with one-third in the low canopy, by June only one-fifth remained in the field layer and four-fifths had ascended to the canopy.

FAMILY SPARASSIDAE

Micrommata virescens (Cl.)

Micrommata: *M. virescens* is the only British representative of this family and is recognizable in all stages. No immatures were taken in 1954; the first specimens were adults, almost 0.1 per square metre being taken from field layer in May, 1955. Immatures reached greatest abundance (0.2) in August, small numbers being taken until late autumn and again in early spring. Only four adults were taken in May, 1956, and no immatures were found for the remainder of that season. This area may constitute a marginal environment for the species.

FAMILY THOMISIDAE

Diaea dorsata (Fabr.); *Misumena vatia* (Cl.); *Xysticus cristatus* (Cl.); *X. lanio* C.L.K.; *X. ulmi*, (Hahn); *X. luctuosus* (Bl.); *Oxyptila atomaria* (Panz.); *O. trux* (Bl.); *Philodromus dispar* (Walck.); *P. aureolus* (Cl.); *P. rufus* Walck.; *Tibellus oblongus* (Walck.).

Diaea: *D. dorsata* is the only British representative of this genus and is easily recognized in all stages. Abundant in field layer and low canopy; also found in adjacent strata. Peak of density 2.0 at end of July. Peak of adults 0.6 in June. *Misumena*: *M. vatia* is the only British representative of this genus and is easily recognized in all stages. Not abundant, but taken occasionally from field layer throughout summer. Adults from July to October. *Xysticus*: greatest abundance of immatures (1.1 in mid-May) in field layer and low canopy. Adult females of all species from May to October, with peak in late May and early June, when males are also present. *X. cristatus* (0.55 in June) and *X. lanio* (0.42 in June) were only species exceeding 0.1 as adults. *Oxyptila*: taken only at wide intervals from field layer. Adults of both *O. atomaria* and *O. trux* in June. *Philodromus*: greatest abundance (2.2 in early August) in field layer and low canopy. *P. dispar* (0.69 in May), *P. rufus* (0.63 in June), and *P. aureolus* (0.22 in June) were all common as adults. The abundance of *P. rufus* is surprising as this species is generally considered rare in Britain. This record was questioned by Mr. G. H. Locket who confirmed the determination of two specimens and concluded that this must constitute a very localized population of the species. *Tibellus*: the distribution of *Tibellus* was not uniform over the area. At the lower, damper end of the area the population density reached 0.17 in the field layer in early June, whereas at the drier end *Tibellus* was virtually absent. The mean maximum density for the whole area was low at 0.08. A few adults of *T. oblongus* were taken in July.

FAMILY SALTICIDAE

Salticus scenicus (Cl.); *Heliophanus flavipes* C.L.K.; *Europhrys frontalis* (Walck.); *Evarcha falcata* (Cl.).

The family was poorly represented in the area, all species together never approaching a density of 0.1. *Salticus* taken at rare intervals from low canopy, adults in July; *Heliophanus* from mossy areas of ground surface, adults in May; *Europhrys* from field layer, adults in June; *Evarcha* from sunny areas of field layer in early spring, adults May and early June.

FAMILY LYCOSIDAE

Lycosa pullata (Cl.); *L. nigriceps* Thor.; *L. lugubris* (Walck.); *Tarentula pulverulenta* (Cl.); *Trochosa ruricola* (Deg.); *T. terricola* Thor.; *T. spinipalpis* F.O.P.-C.

Lycosa: this is the only genus of the family abundant in the area. Immatures reached greatest abundance (6.68) for a short period in July, just after peak of egg hatch. Adults of *L. pullata* (1.8 in June) and *L. lugubris* (1.7 in June) were very conspicuous in ground zone in the spring, when females were observed sunning their egg sacs on exposed surfaces. *Tarentula* and *Trochosa*: these genera were represented in the samples by adults only. A single male of *T. pulverulenta* was taken in May, one female of *T. ruricola* in early June, and one male and one female of *T. terricola*, and one male of *T. spinipalpis* were taken in May and early June respectively, all from ground zone. These species were probably accidental visitors from nearby meadow communities.

FAMILY PISAURIDAE

Pisaura mirabilis (Cl.)

Pisaura: *P. mirabilis* is the only British representative of the family and is recog-

nizable in all stages. Greatest density of immatures 0.37 in June in the field layer. Peak of adults 0.16 in May.

FAMILY AGELENIDAE

Amaurobius atropos (Walck.)

Amaurobius: only one species was taken in the samples. *A. atropos* was not taken frequently in the immature stages. It commonly builds its web in the root crotches at the bases of trees and these areas were inadequately sampled. In March and April, however, the adults of both sexes seem to wander and were taken in field zone samples. The peak of adult abundance occurred in early April, but they never achieved a density of 0.1.

FAMILY THERIDIIDAE

Theridion vittatum C.L.K.; *T. varians* Hahn; *T. neglectum* Wiehle; *T. melanurum* Hahn (these last two are *T. denticulatum* (Walck.) of Locket and Millidge, separated in 1952 by Wiehle); *T. pallens* Bl.; *Enoplognatha ovatum* (Cl.) (*Theridion ovatum* (Cl.) in Locket and Millidge).

Theridion: ninety per cent of immatures were *T. pallens*. This small spider is distinctive and easily recognized in all stages. Taken from all strata, with a peak abundance of 8.8 as immatures in August, and 1.92 as adults in June. This is the most abundant species in the area. A single female of *T. melanurum* taken from low canopy. This specimen, determined by Locket, was a surprising find, as the species is usually confined to the vicinity of buildings. Peak abundance of immatures other than *T. pallens* was 0.92 in June. Peak abundances of adults were: *T. vittatum* 0.10 in June, *T. neglectum* 0.13 in July, *T. varians* 0.11 in July. *Enoplognatha*: the single species, *E. ovatum*, occurred at intervals in long field layer vegetation but never achieved a density of 0.1. Adults in late July and August.

FAMILY TETRAGNATHIDAE

Tetragnatha montana Sim.; *T. obtusa* C.L.K.; *Pachygnatha clercki* Sund.; *P. degeeri* Sund.

Tetragnatha: peaks of immatures were 1.72 in August 1955 and 1.76 in June 1956, in the high foliage of field layer and in low canopy. Adults of *T. obtusa* reached greatest density of 0.19 in third week of July, mainly in the field layer; adults of *T. montana* 0.46 one week earlier, mainly in low canopy. *Pachygnatha*: immatures rare, in field layer. Two *P. clercki*, one of each sex, and one male *P. degeeri* were collected in two years of sampling.

FAMILY ARGIOPIDAE

Meta segmentata (Cl.); *M. segmentata mengei* (Bl.); *M. merianae* (Scop.); *Araneus gibbosus* (Walck.); *A. diadematus* Cl.; *A. marmoreus pyramidatus* Cl.; *A. cornutus* Cl.; *A. umbraticus* Cl.; *A. triguttatus* (Fabr.); *A. inconspicuous* (Sim.); *Cercidia prominens* (Westr.); *Cyclosa conica* (Pallas); *Zygiella atrica* C.L.K.

Meta: immatures common all summer; two peaks of abundance, one in late May and early June with a maximum of 1.37 in June, and one in mid-August with a maximum of 2.33, mainly in high vegetation of field layer and in the low canopy. *M. merianae* adults in May to July with a peak of 0.096 in June, mainly in field layer; *M. segmentata mengei* from late May to mid-July in small numbers in field layer; *M. segmentata* from late July to November with peak of 0.75 in October, mainly in low canopy. *Araneus*: immatures from April to December in low

numbers. Maximal density in May 1955 with 0.81 and in June 1956 with 1.26. Abundances of adults were: *A. gibbosus* 0.14 in June, in field layer; *A. inconspicuous* 0.45 in May in low canopy; *A. diadematus* 0.41 in September in field layer and low canopy. Remaining species never achieved a density of 0.1. All species are fairly common but individuals are widely spaced. *Cercidia*: immatures taken only at wide intervals. One female *C. prominens* from low canopy in July. *Cyclosa*: immatures at wide intervals. Three males and two females taken from field layer in late April. *Zygiella*: immatures common all summer with peak abundance of 0.74 in May, in field layer. Adults of *Z. atrica* in late September or October; peak abundance 0.11 in mid-September, mainly in the low canopy but also abundant in the field layer.

FAMILY LINYPHIIDAE

(As the nomenclature of Locket and Millidge is followed in this paper, family Linyphiidae will conform to their concept and include two subfamilies, the Linyphiinae and the Erigoninae. Most modern authors, however, divide this large group into two families, the Linyphiidae and the Micryphantidae.)

SUBFAMILY ERIGONINAE (MICRYPHANTIDAE)

Ceratinella brevis (Wider); *C. brevipes* (Westr.); *Cornicularia cuspidata* (Bl.); *Gongylidium rufipes* (Sund.); *Hypomma cornutum* (Bl.); *Gonatium rubens* (Bl.); *G. rubellum* (Bl.); *Maso sundevalli* (Westr.); *Tapinocyba praecox* (O.P.-C.); *Micargus herbigradus* (Bl.); *Panamomops sulcifrons* (Wider).

Immatures of this subfamily are difficult to tell apart, and identification even to generic level is unreliable. Immatures of the group, representing at least 11 species, are abundant at all times, with peaks of 7.74 in 1955 and 10.36 in 1956, in June for both years. Five species, *C. brevis* (0.12 in October), *C. cuspidatata* (1.5 in September), *G. rufipes* (0.70 in October), *H. cornutum* (1.09 in June, 1955 and 0.42 in July 1956), *G. rubens* (0.35 in August), constituted over 80 per cent of the adult population of Erigoninae. Though all of these are small and are confined to the ground zone and low field layer, where they are not readily observed, they constitute an important part of the spider fauna. Sweeping brings them to light in large numbers, but recent tests with a suction collecting device by Dr. E. Schlinger, Citrus Experiment Station, Riverside, California (personal communication), and since confirmed by myself, indicate that sweeping collects only a fraction of the Erigoninae present in the ground zone.

SUBFAMILY LINYPHIINAE (LINYPHIIDAE)

Bathyphantes nigrinus (Westr.); *Centromerus sylvaticus* (Bl.); *Drapetisca socialis* (Sund.); *Floronia bucculenta* (Cl.); *Labulla thoracica* (Wider); *Stemonyphantes lineatus* (L.); *Lepthyphantes minutus* (Bl.); *L. tenuis* (Bl.); *L. zimmermanni* (Bertk.); *L. cristatus* (Menge); *L. flavipes* (Bl.); *L. ericaeus* (Bl.); *Helophorus insignis* (Bl.); *Linyphia triangularis* (Cl.); *L. montana* (Cl.); *L. clathrata* Sund.; *L. pusilla* Sund.; *L. peltata* Wider; *L. hortensis* Sund.; *L. impigra* O.P.-C.

Immatures abundant all summer with peaks in June, 1955 (4.60) and July, 1956 (6.27), mainly in the field layer but also commonly in the canopy. Of the 20 identified species only seven occurred as adults more frequently than 0.1: *L. minutus* (0.81 in June, 1955 and 1.48 in July, 1956); *L. triangularis* (1.43 in 1954 and 2.23 in 1955, both years in October); *L. impigra* (0.49 in October, 1954 and 0.80 in September, 1955); *L. tenuis* (0.92 in 1955 and 0.49 in 1956, June); *S.*

lineatus (0.13 in 1955 and 0.07 in 1956, April); *B. nigrinus* (0.12 in 1954 and 0.07 in 1955, October); *D. socialis* (0.15 in 1954 and 0.11 in 1955, September).

Where field-layer vegetation grew high and dense the webs of the Linyphiinae formed a virtually continuous sheet of gauzy silk over the grass, herbs and low shrubs. In late summer it was common to find layers of sheet webs spaced at about eight inches to one foot vertical distance apart, sometimes in as many as five or six layers. In such areas the webs present a seemingly impenetrable maze of silken lines from the soil surface to the tops of plants. At densities such as these, the Linyphiinae would seem to play a major role in the mortality of other arthropod members of the community.

Summary

A stand of oaks in a mixed deciduous forest in England was examined to determine the abundance, the species composition, and the distribution of the spiders occurring therein. Only those parts of the area occupied by spiders in their periods of activity were sampled. The numbers of active spiders were very low from mid-January until mid-March. In the spring numbers rose steeply to a mid-summer peak, then declined slowly until early fall. A second peak of abundance occurred in October and was followed by a steady decline to low levels for the winter months. First activities in the spring started in the field layer and moved progressively upward, and this sequence was reversed in the autumn. The biomass of spiders followed closely the pattern of abundance until the first peak of abundance was reached. From this point biomass continued to rise, reaching a peak in September which corresponded to the lowest point of summer abundance. Thereafter biomass declined sharply to low winter levels. Although abundance was significantly higher in 1956 than in 1955, biomass was lower in 1956. The causes of seasonal variations in abundances and biomasses are discussed.

While the numbers of individuals are fairly evenly distributed between the ground zone, the field layer and the canopy layers, the population density of the ground zone is twice that of the field layer, and eight times that of the canopy layers. There is a strong tendency for species to stratify in the structural layers of the forest, but species tend to extend beyond preferred strata and invade adjacent strata. The main zone of species demarcation is the field layer; species from below this layer invade it from beneath, but do not venture higher; species from above invade the layer from above but seldom venture lower. In addition, the field layer has its own fauna, which in turn tends to invade adjacent layers.

Ninety-eight species representing 15 families were taken in the samples. These are listed and briefly discussed.

Acknowledgments

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Design and Efficiency of Mosquito Traps Based on Visual Response to Patterns

By W. O. HAUFE[1] AND L. BURGESS[2]

Introduction

Extensive investigations on the biology and control of biting flies were conducted in northern Canada from 1947 to 1953 (Brown, *et al.*, 1951; Haufe, 1952; Hocking *et al.*, 1950; Twinn *et al.*, 1948, 1950; Twinn 1950). The difficulty of assessing populations of mosquitoes both in chemical control and in ecological investigations limited the interpretation of some of the work that was undertaken. One of the primary objectives of ecological and behaviour studies was to determine the weather conditions that are favourable for attraction of mosquitoes to man. Reliable estimates of the unattracted population must, for this purpose, be obtained independently of the observer. Large catches are also important in estimating abundance when the time for individual catches is reduced to one hour or less. For these reasons a satisfactory mechanically-operated device for sampling mosquitoes in flight became essential.

We initially considered the addition of an automatic separating device to the New Jersey mosquito trap (Headlee, 1932); but in preliminary trials at Fort Churchill, Manitoba, the traps failed to attract mosquitoes during the night. This failure in the Subarctic cannot be related to species composition since *Aedes communis* (Deg.), which is readily caught at night in southern Ontario, is common in the Fort Churchill populations. It appeared to be caused either by a reversal in the behaviour of mosquitoes to light between high and low latitudes or, more probably, by the high natural light intensity during subarctic nights. There is twilight for approximately three hours at Fort Churchill during the longest day in summer, but no period of total darkness. The bright northern horizon during twilight hours may prevent mosquitoes from orientating efficiently to ordinary light traps.

In any case, there are two serious limitations in the use of light traps for quantitative studies on populations. First, light traps can be operated only at

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night whereas many species are active during daylight. Secondly, the volume of air space from which mosquitoes are attracted to a light cannot be defined. Attraction to a small, bright source of light depends on the relation between intensity and the state of adaptation in the eye. Therefore, mosquitoes might exhibit positive or negative phototaxis at variable distances from light traps depending on the intensity of natural light. Robinson (1952) discussed the latter problem and showed also how some insects may congregate at particular distances from the light source under certain conditions. He has pointed out the need for careful consideration of the behaviour of insects in interpreting samples from light traps.

The work of Autrum (1949) and Gaffron (1934) on visual responses of insects to light and to illuminated patterns suggested that attraction to moving patterns might be incorporated in the design of a trap for mosquitoes. This approach was especially promising, since insects respond to patterns of colour or light intensity only when the elements subtend ommatidial angles above a certain minimum that is characteristic of the species. Attraction to a trap using this principle can be defined in terms of a unit volume of air space with the trap at its centre. Variations in the response of insects would seem to depend on visual acuity. In practice, the accuracy of the trap would depend on a design that functions equally at all times of the day under changing light conditions. Theoretically, the basic problem in standardizing this type of trap under both light and dark conditions is the maintenance of optimum or near-optimum illumination in relation to rate of displacement of the pattern.

The purpose of this paper is to describe the development of a trap for mosquitoes using response to moving patterns as the principle of attraction; to give results of some tests on the efficiency and accuracy of the design in attracting mosquitoes under different conditions of illumination; and to briefly describe some models that trapped large samples of mosquitoes in parts of Canada where light traps were unsatisfactory.

Attraction to Illuminated Patterns

Review

Several workers (Autrum, 1949; Gaffron, 1934; Hecht and Wolf, 1929; Hundertmark, 1937; Kennedy, 1939; Knoll, 1926; Rao, 1947; Wolf, 1933; Zerrahn, 1933) have demonstrated consistent attraction in insects to moving patterns and response to flickering intensity of light. The responses described for experimental conditions in the laboratory have not been fully investigated in the field for large variations in natural light intensity, especially in species that depart from typical diurnal or nocturnal rhythms of activity. The rate of adaptation to changing light in some species may be of a very high order, in which case the rate of change of natural light would have no significant effect on attraction to a conspicuous pattern. Autrum (1950) states that eyes in Diptera have a low sensitivity to pattern discrimination but a rapid rate of adaptation mainly suited to the role of flight as the main means of locomotion. This relationship between pattern discrimination and rate of adaptation enhances the use of visual responses in the attraction of flying insects to a trap. A pattern and rate of displacement that facilitate maximum discrimination may provide attraction with adequate uniformity between day and night for some species without critical control of intensity and quality of illumination. On the other hand, if the intensity and quality of illumination significantly affect the power of some insects, even in the adapted state, to distinguish a given pattern from its background, then the amount

of attraction can be kept within closely defined limits only at night and the principle of visual response has little value in a quantitative method of insect trapping.

Spectral sensitivity varies between species of insect. Some insects choose colours mainly in the green to blue whereas others have a bimodal response with the greater peak in the blue to violet-purple and the lesser in the red to yellow portion (Wigglesworth, 1950, p. 146). Gjullin (1947) described the effect of clothing colours on the rate of attack of *Aedes* mosquitoes and presented the view that colours are chosen on the basis of their spectral reflectances and not by ability to distinguish colours. Brown (1951, 1954) presented data that confirmed Gjullin's view. Test colours in Gjullin's and Brown's experiments had a mutual relationship with competing patterns in the surrounding environment. Other work on the responses of animals (Rao, 1947; Knoll, 1921, 1926; Hundertmark, 1937; Schlegtendal, 1934) has indicated that competing environmental patterns in this case may cause variation in ability to select particular colours. Moreover form perception may be superior to colour perception in attraction of flying insects. If this is the case, a trap using a pattern of superior form and contrast might provide uniform or nearly uniform catches with relative independence of natural variations in intensity of illumination.

Method

Preliminary field tests were made at Fort Churchill, Manitoba, in 1951 to study the efficacy of a pattern in attracting mosquitoes and to determine the variations related to intensity and quality of illumination. A high velocity electric motor with fan was mounted at the bottom of a cylinder supported by legs (Fig. 5, D). The top of the cylinder was covered with a circular board, of slightly larger diameter, divided into three equal sectors separated by radial partitions one inch high (A). Each sector was covered by highly reflective white glazed paper. Slits $1\frac{1}{2}$ inches long and $\frac{3}{8}$ inch wide were cut in each of the three sectors to present a random pattern of rectangles on a white field (B). The number, distribution, and orientation of the slits were identical for all three sectors. A screen mesh funnel connected the lower surface of each sector to a separate cyanide killing jar mounted on the inside wall of the cylinder above the fan. In operation, the fan provided a strong suction through the slits and screen funnels and past the cyanide killing jars. Mosquitoes landing on the upper surface of sectors were sucked through the slits into the screen funnels where they were narcotized and subsequently collected in the killing jars. A light bulb was mounted six inches above the landing surface and midway in the arc of each sector with a shade that confined its illumination to the sector directly below (C). When landing surfaces were illuminated in semi-darkness, the slits appeared black in contrast to the paper surface.

The device was operated on 13 nights between June 26 and July 22, 1951, when the black-legged species of *Aedes* were near their peak of abundance. During this period at Churchill, the sun sets after 2100 hours and the period of civil twilight[4] varies from 2.6 to 2.9 hours. The sampling period for each night was arbitrarily limited to one and one-half hours between 2345 hours and 0115 hours to utilize maximum darkness. Only a portion of this period was represented by nearly total darkness, but the sampling period could not be restricted further without affecting the significance of the mosquito catches. An attempt was made to sample mosquito populations on all cloudy nights for

4A limit is usually fixed at a solar depression of 6° below the horizon and the time interval between this point and sunrise or sunset is called 'civil twilight'.
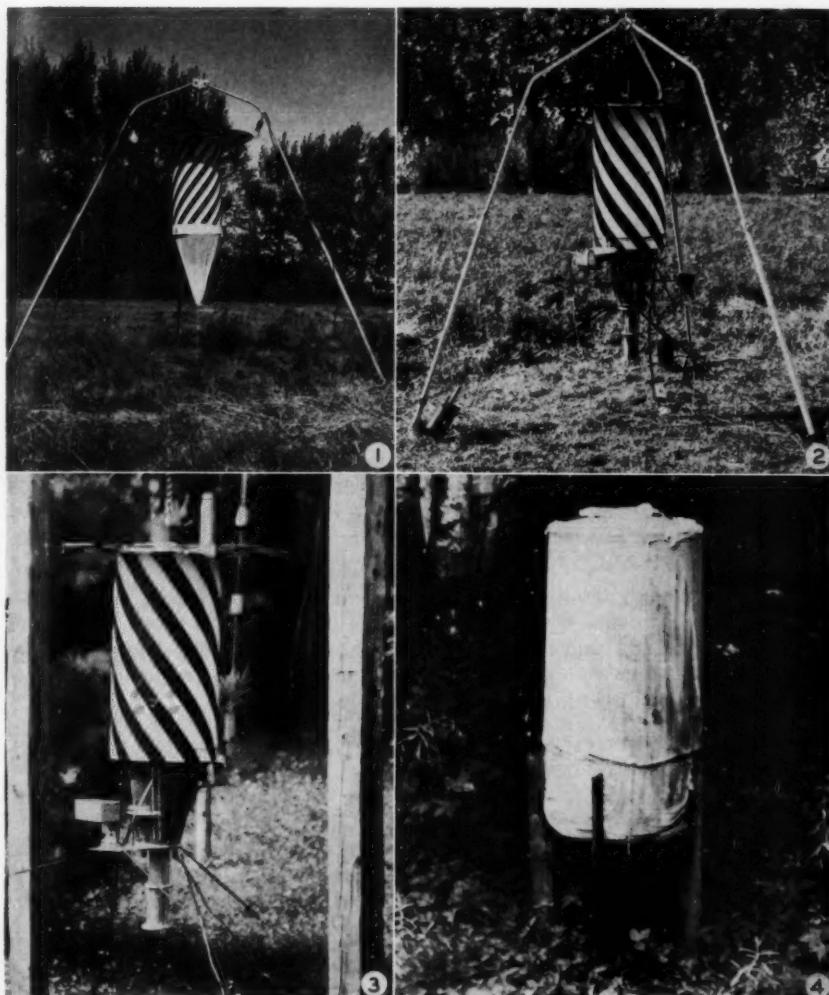
Figs. 1-4.   1. Simple model of the visual-attraction trap in which mosquitoes are collected in a standard sweep net. 2. Trap supported by collapsible and adjustable tripod. The shaded lights with collimators to confine the light to the cylinder at night are shown attached to the bases of the tripod legs. 3. Trapping site at Rowanton Depot, Quebec, showing the visual-attraction trap in relation to surrounding vegetation. 4. Trapping site of the suction trap operated in the efficiency trials at Rowanton Depot, Quebec.

the same reason. The trap was placed in an open area and rotated 120° at the end of each 30-minute period so that the sectors of the landing surface would be equally exposed to the windward and leeward sides each night. Since direction and velocity of wind, apart from gustiness, were fairly steady during any of the test periods, it is unlikely, with this precaution, that wind affected the overall results to any serious extent. The intensity and quality of light from a 60-watt white, frosted light bulb was used as the standard for illumination in

TABLE I

Physical characteristics of surface illumination and light sources used for attraction of
mosquitoes to surface patterns

Bulb colour	Power (watts)	Light characteristics of landing surface at 6 inches from the light source		
		Brightness (log. foot-lamberts)	Incident illumination (foot-candles)	Reflection factor*
Standard white	60	2.82	208	.480
Light blue	100	3.05	404	.738
Dark blue	60	2.71	164	.724
Light yellow	100	3.11	410	.776
Dark yellow	60	2.74	176	.632
Bright white	100	3.29	617	.851

*The ratio of the brightness of a given surface to that of a magnesium carbonate block.

all comparisons. The standard bulb was compared with a light blue and a light yellow for the first five test periods and with a dark blue and a dark yellow for the following six. The physical characteristics of illumination from the bulbs are described in Table I.

Since some insects choose colours mainly in the green to blue whereas others have a bimodal response with the greater peak in the blue to violet-purple and the lesser in the red to yellow portion of the spectrum, the choice of bulbs was considered to have sufficient range in quality of light to demonstrate variations in attraction to artificially-illuminated landing surfaces.

Results

The relative abundance of species changed during the season. The early-season population complex was almost entirely composed of black-legged species, but large numbers of banded-legged species appeared in late summer as the total population gradually declined. Moreover, seasonal changes in populations correspond to changes in the general flight activity of females (Haufe, in preparation). Therefore, catches of mixed species were directly comparable for different days only during the early season when populations were predominantly represented by the black-legged group (*Aedes impiger* (Walk.), *A. punctor* (Kirby), *A. hexodontus* Dyar, *A. nigripes* (Zett.) and *A. communis* Deg.). Catches 1-11 in Table II represented this period. Catches during periods following the first 11 contained increasing numbers of the banded-legged species. Subsequent sampling in other studies in the field showed a normal seasonal decline in abundance for the general populations with increasing proportions of late-season species. Therefore the analysis of results was limited to catches during the first 11 sampling periods.

The catches shown in Table II cover a period with the variable weather conditions that are normally encountered during the mosquito season at Churchill. The landing surface was oriented in three directions with respect to wind: windward, leeward and cross-wind. Sample No. 12 is included to show that the combination of bright white, light blue, and dark blue was of the same order as that for the combination of standard white with light blue or dark blue. The lower catches for both yellows in relation to those for other qualities of light are obvious by inspection. Statistical analysis was designed to test two

TABLE II

Catches of mosquitoes attracted to patterns under different colours of illumination in relation to weather

Sample period	Weather conditions			Trap catches per 1½ hours			
	Temperature	Moisture	Cloud cover	Standard white	Light blue	Light yellow	Total
No. 1	Cool	Dew	Clear	105 (W)*	117 (L)*	46 (C)*	268
2	Cool	Dew	Clear	190 (C)	187 (W)	92 (L)	469
3	Cool	Dew	Clear	341 (L)	371 (C)	277 (W)	989
4	Cool	Dew	Clear	321 (W)	289 (L)	211 (C)	821
5	Warm	Humid	Nimbus	489 (C)	503 (W)	343 (L)	1335

Peak of general abundance

	Temperature	Moisture	Cloud cover	Standard white	Dark blue	Dark yellow	Total
6	Warm	Humid	Overcast	437 (L)	341 (C)	127 (W)	905
7	Cool	Dew	Clear	218 (W)	262 (L)	133 (C)	613
8	Very warm	Brief showers	Overcast	767 (C)	538 (W)	187 (L)	1492
9	Cool	Dew	Clear	87 (L)	104 (C)	46 (W)	237
10	Very warm	Brief showers	Overcast	648 (W)	682 (L)	284 (C)	1614
11	Cool	Dew	Clear	158 (C)	203 (W)	132 (L)	493
				Bright white	Light blue	Dark blue	
12	Warm	No dew	Clear	263 (L)	291 (C)	241 (W)	795

Cool—below 50° F.; Warm—50-65° F.; Very warm—above 65° F.

*(W), (L), (C) denote the orientation of the landing sector to windward, leeward, cross wind, respectively, for the first 30-minute period each night.

aspects of variation.   First, differences were tested with Student's t to interpret variations in relation to quality of illumination.   Secondly, the catches were tested for homogeneity of the populations.   The results of these tests are shown in Table III.   Real differences between catches were established for the dark yellow as compared with standard white and dark blue.   The tests also suggested differences for light yellow as compared with standard white and light blue. $^-X^2_-$ tests showed that the populations sampled in successive periods were nearly homogeneous only for the standard white and light blue illumination in the first five sampling periods.

Rearrangement of the data in relation to speed and direction of wind is shown in Table IV.   A difference in the average ratio of windward to leeward catches was observed for low wind velocities of zero to six as compared with higher velocities above eight miles per hour, but this difference was not statistically significant in relation to the large variation between catches for different sampling periods.

Discussion

The existence of a continuously changing species complex in populations throughout the mosquito season was recognized in the design of all field tests. Other correlations of mosquito behaviour in the field have indicated that, generally speaking, relations between flight and attraction to man are similar for the early-season species in the black-legged *Aedes* group (Haufe, in preparation).   If the early-season species are equally comparable in their thresholds of visual response, considerable homogeneity might be expected in the mixed populations during the early part of the season, i.e., during the 11 sampling periods described.   Statistical analysis has shown that an unexpectedly high level of variability exists even in the early populations.   However, this heterogeneity may not be related to species differences in the black-legged group so much as to intraspecific differences that are related to age and previous activity.   Laboratory experiments on the response of stabilized colonies of *A. aegypti* (L.) have shown that thresholds for stimulation by physical factors in the environment vary with age, starvation, and the time and amount of previous activity (Haufe, 1958).   In view of the variety of environmental conditions prevailing for different sampling periods in the field tests, it is more likely that the heterogeneity between catches is related to intraspecific variations in visual response in populations over the mosquito season.   If this is true, catches would tend to be selective for certain age groups depending on the quality of pattern illumination and on previous activity.   Critical testing of visual response to patterns as a principle in mosquito trapping appears to require laboratory tests based on homogeneous populations, especially in relation to age and starvation.   Although our preliminary field tests are inconclusive in some respects, they provide grounds for speculating on the variations that may be expected in catches attracted to patterns.

Intraspecific heterogeneity in population response may also account primarily for the lack of statistical significance of the differences related to speed and direction of wind in Table IV.   Regular orientation of the trap for nightly catches would eliminate major variation in suction efficiency between sectors and in orientation of mosquito flight at high vs. low wind speeds, but it would not eliminate intraspecific variation in response thresholds for wind for consecutive nightly catches.   The tests have shown that in trap design attraction to a pattern should be omnidirectional for efficient operation in variable wind conditions.

TABLE III

Comparison of catches from landing surfaces with different qualities of illumination

Comparisons				Probability	
Light*	Total mosquitoes		No. of samples	Difference ('t') test	Homogeneity (X^2)
SW vs. LB	1446 vs.	1467	5	> .9	> .7
SW vs. LY	1446 vs.	969	5	> .2	< .001
SW vs. DB	2315 vs.	2130	6	> .7	< .001
SW vs. DY	2315 vs.	909	6	< .05; > .02	< .001
LB vs. LY	1467 vs.	969	5	> .2	< .001
DB vs. DY	2130 vs.	909	6	< .05; > .01	< .001

*Standard white (SW); light blue (LB); light yellow (LY); dark blue (DB); dark yellow (DY)

The assumption that perception of form can be made the primary factor in the function of a visual-attraction principle in trap design appears to be justified by field tests within certain limits. The difference between sectors in the quality of the surface illumination influenced attraction of mosquitoes considerably less than the difference in contrast between the landing surface and its pattern of rectangular apertures. The results of analyses in Table III indicate that attractiveness of the sectors was primarily dependent on change of retinal stimulation as the mosquitoes flew over the pattern of dark apertures. Backgrounds illuminated with yellow light were less perceptible to the mosquito than the others and the difference in attraction appeared to be inability to distinguish a contrast between the apertures and the landing surface when the

TABLE IV

Effect of wind direction and speed on mosquito catches from an illuminated landing surface

Sample period	Wind speed (mi./hr. at 30 ft. above ground)		Catches of mosquitoes/1½ hours*			Ratio of windward to leeward catches	Total
			Windward	Leeward	Cross wind		
No. 8		0– 2	394	572	526		1492
9		1– 3	69	97	71		237
3	0–6	3	299	379	311		989
7		4– 5	201	215	197		613
1		5	72	118	78		268
2		4– 6	141	166	162		469
Average			196[1]	258[1]	224	.76	
No. 4	6–8	6– 8	293	259	269		821
11		7– 8	153	182	158		493
Average			223	220	213	.98	
No. 5		8– 9	451	416	468		1335
10	>8	8–10	555	507	552		1614
6		11–14	321	263	321		905
Average			442[2]	395[2]	447	1.12	

*Total of three, 30-minute catches for each sampling period; one from each of the white, blue, and yellow landing surfaces.

Probability of difference: [1](.6), [2](.7).

latter was illuminated with light in the red end of the spectrum. Lack of correlation between differences in catches and reflection factor, incident illumination, and brightness also accords with this view. The dark yellow fell between standard white and the blues for reflection factor, between dark blue and light blue for incident illumination, and between standard white and dark blue for brightness (Table I). The difference in catches between yellow and the other colours of illumination cannot be attributed to any of the three measurements of quality unless there are two sets of thresholds for stimulation of the mosquito eye. The only likely explanation for these results is that trapped mosquitoes responded to transitory stimulation (Wolf, 1933) by the pattern of slits on the landing surface. The low catches for yellow illumination would indicate that the perception of difference between black and yellow for the mosquito is near the lower threshold for perception of contour between contrasting surfaces.

Studies of visual responses in insects have frequently demonstrated a response to the displacement of a pattern within the visual field. For example, if bees are permitted to choose among series of patterns of the same area but of different design, the number of choices of each pattern is proportional to the lengths of their contours (Zerrahn, 1933). Sippell and Brown (1953) have shown in addition that, while airborne factors of attractiveness predominate in mosquitoes when the host is still, the visual factors predominate when it is in motion. Both Kennedy (1939) and Rao (1947) have demonstrated that mosquitoes orientate toward moving black stripes in the presence of stationary ones. The evidence indicates that the mosquito, like the honey bee, responds to stimulation produced by change of pattern during flight. Wolf (1933) found that in the bee the choices are directly proportional to flicker frequencies of fields of equal size provided the frequencies are below fusion and Wolf and Zerrahn (1935) found two flickering fields to have the same stimulating effect when the product of flicker frequency and area is the same. Since there was no significant difference in attraction to the pattern of a standard landing surface under different qualities of illumination with the exception of yellow and since agreement between catches in white and blue light is highly probable (Table III) even under variable field conditions for several days when heterogeneity in populations increases rapidly with the seasonal build-up of a complex of species and age groups, mosquitoes in flight, like bees, may be considered to respond primarily to changing patterns. If this is so, there are no serious limitations to the use of visual responses in mosquito trapping if the attractiveness of the trap is superior in competition with all other patterns in the environment under various sampling conditions. Theoretically, these conditions are fulfilled if the trap has (1) maximum possible contrast across contours of the pattern, (2) no incident illumination from point sources to interfere with the normal stimulation of the attracting pattern, and (3) a rate of movement providing optimum or near-optimum transitory stimulation. Yellow illumination was an extreme condition tested in our preliminary experiments and it, as well as other ineffective qualities, can be avoided in any trap design requiring artificial illumination.

Trap Designs

Description

A simple model of an omnidirectional trap was constructed and operated at Churchill in 1952 (Fig. 1). It consisted of a black and white spirally-striped cylinder rotating on bearings around a high velocity motor and fan. The trap

was rotated by the pressure of the air stream against vanes attached to the inside wall of the cylinder. Adjustment of the vanes controlled the rate of rotation of the cylinder and consequently the flicker frequency of the stripes. Mosquitoes, orientated by the stripes to the aperture at the top of the cylinder, were forced through the cylinder by the air stream and were collected in an ordinary mosquito net attached to the base. The volume of air space sampled was proportional to the width of the black and white stripes, since attraction of mosquitoes depended on a minimum ommatidial angle subtended by an individual stripe. This model was inexpensive and efficient for sampling populations on a daily basis but manual changing of the net was inconvenient for short-period separation of catches. Necessity for frequent adjustment of the vanes was a further disadvantage. The friction in well lubricated ball bearings varied enough to influence the drag on the vanes and hence to vary the speed of rotation. Regular checking was necessary therefore to regulate the vanes for maintenance of a favourable flicker frequency in the pattern.

A more precise automatic design was developed from the simple model. This trap is illustrated in Figs. 2 and 5E. A high velocity fan mounted in a central framework created an air stream downwards through the trap. The spirally-striped attraction cylinder and disc rotate on ball bearings around a central shaft extending upwards from the central framework. Twelve black and white stripes $1\frac{5}{8}$ inches wide were painted spirally around the circumference of the cylinder. In addition there was a similar number of black and white spiral stripes on both surfaces of the horizontal disc, necessarily expanded toward the outer and narrowed toward the inner edge. The horizontal disc contained a hole at its centre with diameter slightly less than the opening in the upper end of the cylinder to accommodate an air stream. Mosquitoes approaching the cylinder orientated toward the black and white contour lines. Inward spiralling of the pattern on the rotating cylinder directed them toward the opening at the top of the cylinder. The horizonal disc prevented mosquitoes overshooting the top of the cylinder and directed them into the air stream. The cylinder assembly was rotated at the desired constant speed by a belt from a motor mounted on the side of the framework. The upper portion of the framework of the trap was enclosed by galvanized sheet iron, the lower portion by fine copper screening. A replaceable collecting cartridge fitted into the lower end of this framework. The mechanism for separating the samples was a modification of that described by Johnson (1950). The lower portion of the cartridge was made of perforated zinc sheeting, which allowed air to pass through but retained the insects. Sixteen small aluminum discs machined to fit the cartridge were loaded in the upper end. Samples were divided at hourly or other equal intervals by the discs, which were dropped singly down a central rod. Each disc had a central collar to separate one from another and thereby prevent crushing of insects. Collecting cartridges were detachable from the trap and, also, interchangeable for transportation of samples to the laboratory. The number of discs was sufficient to accommodate changes twice daily at convenient times in morning and evening for hourly operation. The disc-dropping mechanism, mounted on the side of the trap, consisted of a selector arm connected to a magnetic plunger that was operated by electrical power through a timing device. Various models of cycle repeaters may be employed in the magnetic plunger circuit to provide sample operation at various intervals of time. An adjustable tubular steel tripod was a convenient support for the trap, especially when frequent changes of location were necessary.

The design of the collecting cartridge and disc-release mechanism in the automatic model was adopted by Harcourt and Cass (1958) in the development of a light trap and has been described by them in greater detail. Engineering blueprints of the complete visual-attraction assembly and parts are on file at the Research Station, Canada Agriculture, Lethbridge, Alberta.

Efficiency

Some observations of the behaviour of mosquitoes around the trap were made, through binoculars, from a point 25 yards away. With a stripe width of 1⅜ inches and a stripe displacement rate of 160-180 per minute, mosquitoes flying in the vicinity of the trap were abruptly orientated to the stripes within a maximum distance of approximately 32 inches from the cylinder. This distance was somewhat reduced for mosquitoes flying either directly above or directly below; thus mosquitoes approximately 18 inches or more above the cylinder showed no distinct orientation and those flying at grass level were not attracted when the bottom edge of the cylinder was four feet above the ground. Observations generally indicated that mosquitoes responded to the pattern at slightly greater distances when flying below than when flying above the cylinder. The abruptness of orientation towards stripes generally increased with proximity to the stripe within the 32-inch effective range of attraction. Mosquitoes approaching within a few inches of the cylinder often circled it rapidly toward the top. They escaped the influence of the pattern by going through the opening between the upper edge of the cylinder and the lower surface of the horizontal disc and into the air stream. Therefore, the catch was a sample of flying mosquitoes that infiltrated a definite air space from any direction. When the rate of displacement of the stripes exceeded 200 per minute, the 'circling' flight increased and became erratic. At high rates of displacement circling flight was replaced in a large number of mosquitoes by 'circus movements' that prevented regular orientation toward the opening in the cylinder.

The simple model of the trap was illuminated from all sides by 40-watt electric lights during periods of low natural light intensity to maintain superior attraction of the striped pattern against the blackground. It captured large samples of all species at Churchill, Manitoba, in 1952. The net was changed hourly from 6:00 a.m. to midnight and the catch for the remaining part of the day was collected as a single sample. Hourly catches ran as high as 830 in the 6:00 a.m. to midnight periods. A catch exceeding 24,000 was taken in one of the early morning six-hour periods when favourable weather led to an unusually prolonged period of flight activity during the peak of seasonal abundance.

Investigations on the biology of mosquitoes were discontinued at Churchill in 1953. The automatic model was tested later at Rowanton Depot in southern Quebec. Mosquitoes in this area consisted of a different association of species, which appeared in order of abundance approximately as follows: *Aedes communis*, *A. fitchii* (F. & Y.), *A. excrucians*, *A. punctor*, *A. intrudens* Dyar, *A. stimulans* (Wlk.), *A. implicatus* Vock., *A. canadensis* (Theo.), and *A. vexans* (Mg.). Field tests were conducted in marginal forest consisting of scattered stands of young spruce, pine, birch, poplar, and shrubs. Because of the uneven topography, the trapping sites were not as uniform as those at Churchill.

An automatic visual-attraction trap (Fig. 3) was operated continuously from June 14 to July 3. The trap was illuminated from three directions at night by 60-watt light bulbs at a distance of 25 feet from the trap. Shields on the light sources confined the incident illumination to the trap cylinder and, also,
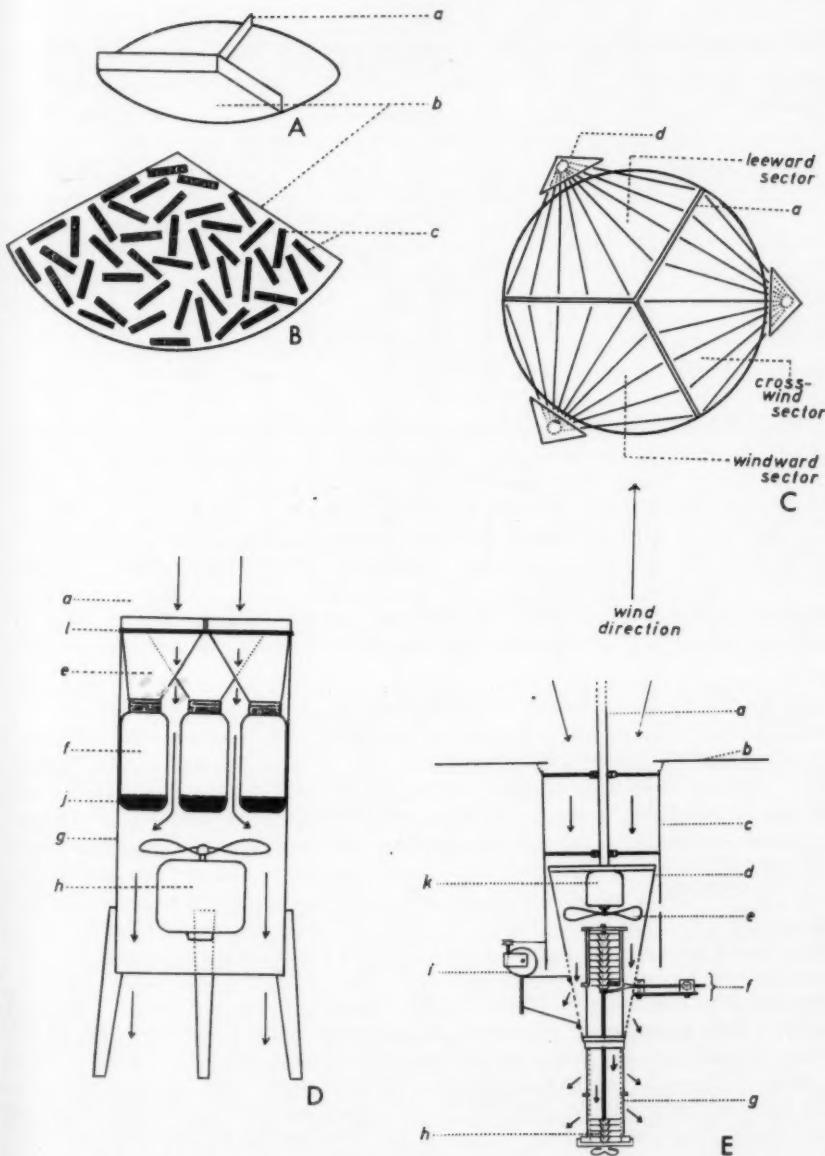
Fig. 5. A-D. The landing surface and trapping cylinder used to compare the effect of quality and quantity of light on the attraction of mosquitoes to a pattern. A, the circular landing surface with vertical dividers; B, one of the three sectors of A, showing pattern of slots; C, top view of landing surface, showing orientation to wind and arrangement of shaded lights; D, sectional diagram of the trapping cylinder. E. Sectional diagram of the visual-attraction trap with sample-separating device. (a) support, (b), horizontal disc, (c) attraction cylinder, (d) framework for collection assembly, (e), fan, (f) disc-dropping mechanism, (g) collecting cartridge, (h) disc with collar, (i) motor for driving cylinder, (k) fan motor. The cylinder turns about the supporting shaft (a) on two ball bearings.

TABLE V

Mosquito catches in visual-attraction and suction traps at Rowanton Depot, P.Q., 1954, with a preliminary estimate of trap efficiency

| Date 1954 | Visual-attraction trap | | | | | | Suction trap | | | | | |
| | Day | | | Night | | | Day | | | Night | | |
	Bl[a]	Ba[b]	To[c]	Bl[a]	Ba[b]	To[c]	Bl[a]	Ba[b]	To[c]	Bl[a]	Ba[b]	To[c]
14 VI	3	0	3	57	4	61	4	1	5	9	6	15
15 VI	15	2	17	87	2	89	1	0	1	6	1	7
16 VI	81	0	81	157	0	157	2	1	3	4	3	7
18 VI	5	0	5	25	3	28	0	1	1	1	2	3
19 VI	3	0	3	54	11	65	0	1	1	14	2	16
21 VI	2	0	2	111	6	117	0	0	0	16	0	16
22 VI	6	0	6	40	6	46	0	0	0	2	1	3
23 VI	4	1	5	5	1	6	0	0	0	1	0	1
24 VI	0	0	0	92	49	141	0	0	0	1	0	1
25 VI	1	0	1	18	18	36	1	0	1	9	1	10
26 VI	4	0	4	12	22	34	0	0	0	3	1	4
27 VI	2	0	2	6	13	19	0	0	0	4	3	7
28 VI	0	0	0	4	5	9	0	0	0	2	1	3
29 VI	0	0	0	17	9	26	0	0	0	0	2	2
30 VI	4	0	4	56	76	132	0	0	0	1	2	3
1 VII	0	0	0	20	83	103	0	0	0	0	1	1
2 VII	1	0	1	5	4	9	0	0	0	2	0	2
7 VII	2	0	1	1	2	3	1	0	1	0	0	0
Total	133	3	136	767	314	1081	9	4	13	75	26	101

Species forms	$\overline{R}_r$[d]	$\overline{R}_s$[e]	Student's t for $(\overline{R}_r - \overline{R}_s)$	D.F.	Probability
Bl	0.192	0.082	1.52	30	<0.2>0.1
Ba	0.097	0.097	approx. 0	24	0.9
To	0.125	0.082	0.702	34	0.5

[a]Bl — black-legged

[b]Ba — banded-legged

[c]To — total

[d]$\overline{R}_r$ — ratio for visual-attraction

[e]$\overline{R}_s$ — ratio for suction

considerably reduced the "dazzle" effect described by Robinson (1952). A suction trap containing a minimum of attractant factors was operated 60 feet away on the opposite side of a thick growth of trees (Fig. 6). It consisted of a metal cylinder, 15 inches x 30 inches, swathed in grey cloth. A dual blower in the bottom of the cylinder provided an air stream, which trapped the mosquitoes in a small insect net hanging from a 6-inch hole in the top of the cylinder.

The catches of *Aedes* spp. in each trap were separated into 'black-legged' and 'banded-legged' forms, since the species in these groups exhibit different diel periodicities in activity (Haufe, in preparation). The latter group tends to be more nocturnal in habits. Catches summarized in Table V show the same general trend throughout the summer for both traps. The visual-attraction trap caught approximately 10 times as many mosquitoes as the suction trap with the exception of 'banded-legged' forms in the daytime. The important question is whether the attraction of mosquitoes to a pattern varies between day and night

TABLE VI

Comparison of catches for homogeneity in relation to species forms

Mosquito forms	Catch	No. in visual trap	No. in suction trap	Total catch	Probability based on X^2
Black-legged...........	day.............	133	9	142 ⎫	
	night............	767	75	842 ⎬	< .5; > .3
	total............	900	84	984 ⎭	
Banded-legged...........	day.............	3	4	7 ⎫	
	night............	314	26	340 ⎬	< .01
	total............	318	30	348 ⎭	
Mixed.................	day.............	136	13	149 ⎫	
	night............	1081	101	1182 ⎬	> .95
	total............	1217	114	1331 ⎭	

for given species. If there is variation, then significant differences should be apparent between the two traps for the ratio of day to night catches. Catches were empirically separated therefore at 0800 and 2000 hours. Tests for the significance of differences between these ratios are given in Table V. Catches recorded in italics could not be tested, since the value of a ratio becomes infinite when the denominator is O. Therefore, the sets of catches that had to be omitted are reflected in the different degrees of freedom for the three statistical comparisons. The ratios for the traps are not significantly different but there is a wide range of probability between the two species' forms and the total catch.

Testing of the traps in the field involved complex sources of variation. Most of these concern the behaviour of different species. Individual species exhibit wide variations in their diel periodicities of activity. These variations are also related to diel periodicities that are characteristic of meteorological factors. These relationships raise criticism of an empirical separation of day and night catches at certain times of morning and evening. Catches of species in which the diel increase of activity occurs near daybreak or sunset are especially difficult to assess in this respect, since variation in the day to night ratio may be a result of shifts in diel periodicity of activity. The seasonal day and night catches for the 'banded-legged', 'black-legged', and combined forms were tested therefore for homogeneity (Table VI). The probability of homogeneity was high for the total mosquito population and the 'black-legged' forms alone. The 'banded-legged' forms were heterogeneous at the one per cent level. In the latter case the day catches were extremely small. This fact, in addition to the general nocturnal behaviour of 'banded-legged' forms, suggested caution in inter- preting results. The 'banded-legged' forms tended to be active in open spaces at night and to rest in vegetation during the heat of the day. The uniformity of the two trapping sites (Figs. 3 and 4) was doubtful, since the suction trap was operated on the ground nearer to trees and vegetation than the visual-attraction trap. Therefore, larger numbers of 'banded-legged' forms would be expected around the visual-attraction trap at night and around the suction trap during the day. The catches for 'banded-legged' forms (Table VI) accord with this behaviour. Catches are being compared more critically between these two types of traps under uniform conditions in alfalfa fields on level irrigated prairie.

The relation between activity within populations and factors of the physical environment, although recognized in all tests, will be described in later papers.

Insects Attracted

The visual-attraction trap caught various insects other than mosquitoes, especially in southern Alberta. No systematic analysis has been made of the collection yet but the following orders and families are well represented:—

Dermaptera	
Odonata	— Anisoptera, Zygoptera
Plecoptera	
Hemiptera	— Miridae, Lygaeidae
Homoptera	— Aleyrodidae
Neuroptera	— Chrysopidae
Trichoptera	
Ephemeroptera	
Coleoptera	— Coccinellidae, Carabidae, Curculionidae, Elateridae
Hymenoptera	— Ichneumonidae, Bombidae
Lepidoptera	— Noctuidae, Arctiidae, Sphingidae, Amatidae, Pieridae, Lasiocampidae
Diptera	— Tipulidae, Chironomidae, Tabanidae, Calliphoridae, Muscidae, Tachinidae, Scatophagidae, Asilidae

Large catches of moths were taken occasionally in daylight hours in late evening and early morning as well as during darkness. Daylight catches coincided with passage of weather fronts.

Summary

A principle of visual-attraction was incorporated in the design of a trap for mosquitoes. Tests in the field indicated that the design was efficient in capturing large numbers of mosquitoes in locations where ordinary light traps were unsatisfactory. Positive 24-hour attraction was achieved by using a black and white pattern that was superior in contrast to competing patterns in the environment. The sampling unit, in terms of air space, depended on the distance between contours in the pattern. Comparison with a suction trap under field conditions showed no significant differences in the ratio of empirically divided day to night catches. Statistical tests showed some heterogeneity in day and night samples in the two traps for 'banded-legged' forms of *Aedes* spp., but this was explained by the variation in behaviour that is known to characterize these forms. Special tests in the field on illumination for night operation showed that a relatively uniform contrast in the pattern could be maintained over 24-hour periods with artificial white light. Illumination in the yellow-red end of the spectrum reduced attraction to the pattern. Sampling of mosquitoes flying in the daytime as well as at night was an advantage in visual-attraction traps. The air space sampled remains constant for different light conditions and it can be restricted, if necessary, to accommodate studies on the flight of mosquitoes in relation to microclimate. A sample-separating mechanism provided catches at short regular intervals of the day.

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New Hymenopterous Parasites of Lodgepole Pine Needle Miners

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In rearings of lodgepole pine needle miners (mostly *Recurvaria milleri* Busck and *R. starki* Freeman) in California and Alberta an undescribed species of Ichneumonidae and two of Braconidae have commonly been recovered.

Apanteles starki new species

This species keys to couplet 51 in Muesebeck's Revision (Proc. U.S. Nat. Mus. 58: 483-576 1921) and closely resembles *A. aristoteliae* Viereck. It differs from *aristoteliae* in having longer and thinner antennae, a much longer and aciculately sculptured second tergite, and in averaging smaller and slimmer.

Apanteles californicus Mues., attacking the same host, may be separated by its very long and thin ovipositor valves (longer than the abdomen). The males may be separated by the color of the femora. In *starki* they are always black, the apices of the anterior two or four being brown or yellow. In *californicus* the femora are usually black with brown sides or brown with the upper and lower edges black. The hind femora are darkest; the front are palest, sometimes only black basally above and below. In the darkest males the hind femora are black but the four anterior femora nevertheless retain their brown sides. There are characters in the shape and sculpture of the mesonotum, scutellum, and basal abdominal tergites but individual variation eclipses the specific differences.

Holotype, ♀.—Length, 2.5 mm. Antenna (2.5 mm.) as long as body, of uniform width to apex; second flagellar joint 3.2 times as long as wide, 14th 1.6 times as long as wide.

Mesonotal punctures fine, shallow and contiguous throughout, surface of mesonotum subopaque and thickly hairy; scutum and scutellum both sloping down toward prescutellar scrobe; the latter thin, sharply defined, foveolate and moderately convex anteriorly; scutellum in same plane as mesoscutum, slightly convex, sparsely and very finely punctate. Propodeum shining and weakly rugulose throughout; areola diamond-shaped, bounded by well-defined carinae, shiny and very weakly sculptured within, the anterior carinae meeting and somewhat shorter than the posterior carinae; costulae very weakly indicated; posterolateral areas with rugulosities tending to form several transverse ridges.

Radius about 1.65 times as long as intercubitus, the two veins meeting at an angle of about 45°; nervellus strongly convex outwardly, slanting strongly inward posteriorly. Outer face of hind coxa weakly irregular, hairy, and shiny; outer dorsobasal area not differentiated; inner hind-tibial spur 0.55 times as long as hind basitarsus; outer spur 0.7 times as long as inner.

First tergite with the sides very slightly divergent posteriorly, but curving together in the apical third; length 1.55 times the greatest width and 1.7 times the apical width, strongly arched longitudinally. Base of first tergite concave, smooth, and polished centrally, longitudinally aciculate laterally; center of first tergite finely rugulose and strongly elevated; apical third rugulo-aciculate laterally; depressed, smooth, and shining centrally. Membranous lateral margins 0.4 times as wide as first tergite at its apex. Second tergite trapezoidal; width of base 1.8 times length; apex 1.5 times as wide as base; grooves delimiting the sides slightly convex; surface granular mediobasally, the remainder covered with aciculations diverging posteriorly. Suturiform articulation weakly arcuate; crossed by aciculations laterally. Third tergite smooth and shining, faintly granular mediobasally; 1.8 times as long as second; remainder of abdominal tergites together about twice as long as third. Hypopygium large in lateral view; apex slightly exceeding that of abdomen; lower margin at least three times as long as third tergite, striated and sharply folded medially, apex acuminate (Fig. 2). Ovipositor sheath twice as long as petiole, slightly decurved, gradually broadening to apex; the latter one-half as deep as greatest depth of hind tibia (Fig. 1).

Black; the following parts yellowish brown: palpi, apical third of anterior femur, anterior tibia, middle tibia above, basal two-thirds of posterior tibia. The following parts dark brown: middle tibia above, apex of hind tibia, all tarsi, stigma and wing veins. Wing base and tegula black; tibial spurs yellowish white; wing membranes hyaline.

Allotype, ♂.—Length, 2 mm. Resembling the holotype except as follows: antenna (3.2 mm.) 1.4 times as long as body, apical joints 0.9 times as wide as basal joints, second joint 3.8 times as long as wide, 14th joint 2.4 times as long as wide. Propodeum and abdominal tergites narrower and less strongly sculptured.

Variation.—Females: propodeum sometimes more shining and less strongly sculptured, with the posterolateral corners highly polished and the anterior margins of the areola poorly defined; abdominal tergites occasionally slightly
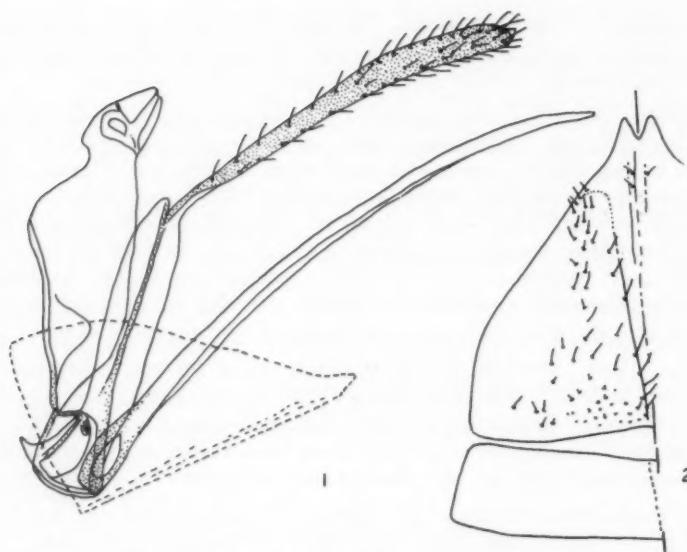
Figs. 1-2. *Apanteles starki*, n. sp. 1, ovipositor; 2, hypopygium.

narrower, suturiform articulation varying from entirely foveolate to narrow and simple. Extreme apex of middle femur and anterior tarsus usually brown or light brown.

Males: sculpture varying like that of females, in extreme cases areola scarcely defined and second tergite as long as broad and almost completely smooth. Legs sometimes darker: in extreme cases only apex of anterior femur, lower side of anterior tibia and small areas at base of other tibiae yellowish brown.

Cocoon.—None were saved, but I would infer from the sizes of the parasite and its host that it is solitary. I suspect that the cocoon is hidden in the mine of the host within the pine needle.

Host.—*Recurvaria starki* Freeman, a needle miner on lodgepole pine (*Pinus contorta* Douglas).

Specimens seen.—24 ♂ ♂, 26 ♀ ♀.

Holotype: Female, Cascade Valley, Banff National Park, Alberta, May 28, 1952, R. W. Stark, reared from *Recurvaria starki* Freeman on lodgepole pine (Canadian National Collection No. 7055).

Hollotype: Male, same data as holotype but June 19 (C.N.C.).

Paratypes: ALTA., 1 ♂, 3 ♀ ♀, same data as holotype but May 28 to June 17 (C.N.C.); 3 ♂ ♂, 3 ♀ ♀, Mt. Girouard, Banff Nat. Pk., June 16-24, 1958 and July 9, 1957 (C.N.C.); 1 ♀, Mt. Massive, Banff Nat. Pk., June 18, 1958 (C.N.C.); 7 ♂ ♂, 4 ♀ ♀, Mt. Eisenhower, Banff Nat. Pk., June 9-18, 1958 and July 22, 1957 (C.N.C.). B.C., 9 ♂ ♂, 9 ♀ ♀, Kicking Horse Valley, Yoho Nat. Pk., June 17 to July 12, 1952 (C.N.C.); 2 ♂ ♂, 5 ♀ ♀, Cathedral Mt., Yoho Nat. Pk., June 16, 1958 and July 1-8, 1956 (C.N.C.). All types were reared by R. W. Stark from *Recurvaria starki* Freeman.
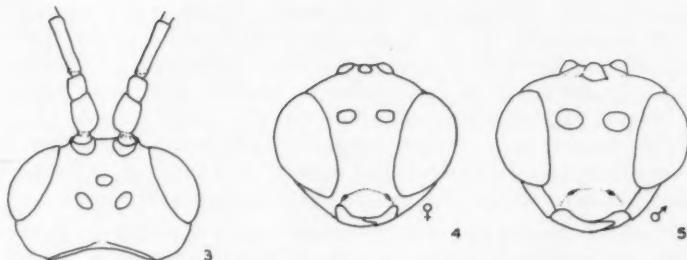
Figs. 3-5. Head of *Meteorus pinifolii*, n. sp. 3, female, dorsal aspect; 4, female, facial aspect; 5, male, facial aspect.

Meteorus pinifolii new species

Meteorus n. sp., Struble, G. R., and W. D. Bedard, 1958. Pan-Pac. Ent. 34: 183.

This species keys to *M. humilis* (Cress.) in Muesebeck's key (1923, Proc. U.S. Nat. Mus. Vol. 63, Art. 2) but differs from that species in many characters. In *pinifolii* the antennae are much longer and thinner, the face is narrower, the eyes larger, the size smaller, as well as numerous other differences. The closest relatives seem to be *tibialis* Mues. and *angustipennis* Mues. It may be separated from *angustipennis* by the longer malar space, larger ocelli, hyaline wings and red abdomen and from *tibialis* and its relatives by the much narrower face, shorter antennae, smaller size and red abdomen.

Holotype, ♀.—Length 3 mm. Head transverse, temple in dorsal aspect two-thirds as wide as eye (Fig. 3); eyes strongly convergent below, the face only three-quarters as wide as long from antennal sockets to base of clypeus (Fig. 4). Clypeus strongly convex, smooth and with only a few punctures; malar space about two-thirds the basal width of a mandible. Face densely and shallowly punctate; frons, vertex, and cheeks, smooth, finely punctate and moderately densely hairy; ocellocular space about 1.5 times the greatest diameter of lateral ocellus. Antenna slender, 24-jointed, a little shorter than body (2.5 mm.); first flagellar joint four times as long as wide; second flagellar joint as long as first.

Sides of pronotum smooth and shining but very finely punctate, the depression somewhat crenulate; propleuron smooth, shining and minutely punctate. Mesonotum shallowly and contiguously punctate, but smooth posteriorly; central lobe not raised above lateral lobes; notauli complete, indefinitely crenulate; area of convergence rugulose; scutellum smooth, with a few shallow punctures; mesopleuron shining, hairy and finely punctate throughout, with a shallow longitudinal groove which is weakly crenulate centrally. Metapleuron shallowly and densely punctate, shining. Propodeum evenly, but not strongly, rounded, its surface weakly and irregularly rugose with some sparse punctures anteriorly; transverse basal carina well developed; transverse apical, and lateral longitudinal, carinae irregular and incomplete.

Wings hyaline; first abscissa of radius half as long as second; second abscissa half as long as second intercubitus; radius reaching the wing margin long before the apex; recurrent vein meeting the first cubital cell well before the apex, the second abscissa of the cubitus one-third as long as the first intercubital. Radiellan cell narrowed apically; lower abscissa of basella as long as nervellus. Posterior coxae shallowly punctate on their outer and upper faces.

Abdomen about as long as head and thorax combined; first segment half as long as rest of abdomen, evenly tapered from the basal 0.2 to the apex; petiole very deep, about twice as deep as wide at the narrowest part; two distinct fossae at the basal 0.2 and a pair of large glymmae laterally, dorsum of petiole longitudinally striate, the striations obsolescent at the apical corners and rugulostriate in the central part; ventral margins widely separated, sternite striated. Second tergite weakly rugulo-granular basally; remainder of abdomen smooth and shining dorsally. Ovipositor sheaths about as long as abdomen.

Light reddish-brown; propleuron, mesopleuron and metapleuron castaneous; prepodeum, metanotum, and base of petiole, black. Antennae, except scape, fuscous. Second tergite suffused with yellow. Legs yellow; hind tarsus and indefinite apical and subbasal annuli of hind tibia, fuscous. Stigma and wing veins yellowish brown.

Allotype, ♂.—Resembling the holotype except in the following details: eyes only weakly convergent below; face much broader, only three-quarters as long as wide (Fig. 5) antenna 28-jointed; sculpture of propodeum and first tergite more irregular. Color of mesopleuron and metapleuron like that of mesonotum, light reddish brown; metanotum, propodeum, and base of petiole dark brown.

Variation.—Females: antennae 24-, to 25-jointed; propodeal carinae often weak, interrupted, or absent; hind coxa usually rugulo-punctate; first abscissa of radius varying from one-third to almost as long as second abscissa; second tergite sometimes sculptured only at anterior corners or, rarely, entirely smooth. Color of mesosternum and propleuron sometimes dark brown; metanotum, propodeum and base of petiole black to dark brown. Canadian specimens much darker in color, upper parts of head, entire thorax, basal 0.9 of first abdominal tergite, hind coxa and usually middle coxa black to dark brown; legs and face brown.

Males: antennae 26-, to 28-jointed; hind coxa usually rugulo-punctate; second abscissa of radius varying from 2.5 to 0.3 times as long as the first abscissa, the second cubital cell subtriangular in the latter cases; second abscissa of radius 0.75 to 0.2 times as long as second intercubitus; second tergite sometimes sculptured only at anterior corners or, rarely, entirely smooth. Color of metanotum and base of petiole light to dark brown; hind legs sometimes entirely yellow. Canadian males much darker in the same way as the females from Canada.

Cocoon.—Peduncle absent; long, cylindrical, and translucent whitish; formed inside the pine needle in the mine of the host. This structure and location is quite unusual for a *Meteorus* but not unique. *M. niveitarsus* (Cress.) forms a cocoon inside the larval feeding tube of its host, *Acrobasis*, and *M. humilis* (Cress.) inside the larval burrows of its coleopterous host.

Host.—Lodgepole pine needle miners, *Recurvaria milleri* Busck in California and *R. starki* Freem. in Alberta.

Specimens seen.—10 ♂ ♂, 32 ♀ ♀.

Holotype: Female, Tenaya Lake, Yosemite National Park, California, emerged July 18, 1953, J. H. McLeod, reared from *Recurvaria milleri* Busck on lodgepole pine (Canadian National Collection No. 7056).

Allotype: Male, same data as holotype (C.N.C.).

Paratypes: CALIF., 7 ♂ ♂, 19 ♀ ♀, same data as holotype (C.N.C.); 7 ♀ ♀, Tuolumne Meadows, Tuolumne Co., July 9, 1955, G. R. Struble, reared from *R. milleri* on *Pinus contorta* (U.S.N.M.); 2 ♀ ♀, same data except July 12,
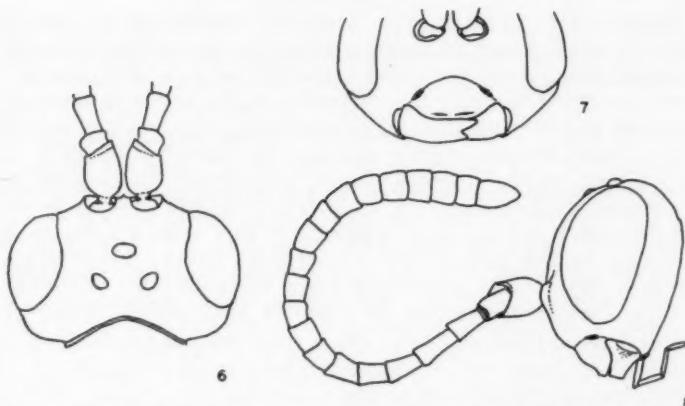
Figs. 6-8. Head of female *Aethecerus pinifolii*, n. sp. 6, dorsal aspect; 7, facial aspect; 8, lateral aspect.

collected by G. L. Downing and R. Stevens (U.S.N.M.). B.C., 1 ♂, Cathedral Mt., Yoho National Park, June 16, 1958, R. W. Stark, reared from *R. starki* Freem. (C.N.C.). ALTA., 2 ♀ ♀, Mt. Eisenhower and Mt. Massive, Banff National Park, June 19, 1958 and June 28, 1956, R. W. Stark, reared from *R. starki* Freem. (C.N.C.); 1 ♂, 1 ♀, Banff, July 1-18, 1949-50 (C.N.C.).

One male from Quebec may belong to this species. The data are as follows: Proulx, Quebec, June 10, 1949, L. Daviault, reared from *Recurvaria piceaella* Kearfott (C.N.C.).

Aethecerus Wesmael

Aethecerus, Wesmael, C., 1844. Tentamen Dispositionis Methodicae Ichneumonum Belgii, p. 203.

This genus is distinguished from *Phaeogenes* by the medially interrupted, subapical ridge on the clypeus (Fig. 7), and by the somewhat expanded apex of the scape (Figs. 6, 8). The small, sharp-pointed process on the hind coxa is also rather typical.

I have seen two North American species belonging here: one is (*Ischnus*) *parvus* Prov. = *Aethecerus parvus* (Prov.) new comb., the other is described below. I wish to thank Mr. J. F. Perkins of the British Museum (Natural History), London, for commenting on this species and suggesting the generic placement.

Aethecerus pinifolii new species

Aethecerus sp., Patterson, J. E., 1921. Jour. Agr. Res. 21: 138.
Phaeogenes sp., McLeod, J. H., 1951. Can. Ent. 83: 298.
?*Phaeogenes* n. sp., Struble, G. R., and W. D. Bedard, 1958. Pan-Pac. Ent. 34: 183-185.

Holotype, ♀ .—Length 4.5 mm. Head in dorsal aspect (Fig. 6) about 1.7 times as wide as long, broadly excavated behind; eye 1.7 times as wide as temple, not prominent; temples convex, converging behind eyes at about 60°. Head in frontal aspect elliptical, about 1.3 times as wide as long; vertex flattened and only slightly elevated above eyes. Face broad, three times as wide as long to base of clypeus, about 0.55 times as wide as head (Fig. 7); inner margins of eyes subparallel; clypeus broadly convex, twice as wide as long, the apex very broadly truncate; subapical ridge extending across central third of clypeus,

absent medially (Fig. 7); malar space about 0.7 times as long as basal width of mandible. In lateral aspect face directed strongly downward, about 30° from the horizontal (Fig. 8); temple of uniform width for most of its length. Ocelli moderately small and flat, forming a broad triangle; stemmaticum neither differentiated nor raised. Occipital carina meeting the hypostomal well above its lower end. Head strongly shining and sparsely, though moderately coarsely, punctate; clypeus highly polished, almost impunctate; area around antennal sockets coriacious. Antennae (Fig. 8) short, about half as long as body, the flagellum 18-jointed and becoming gradually thicker toward apex; apical joints about 1.5 times as wide as basal ones, but only 0.6 to 0.8 times as long; second joint twice as long as wide, penultimate joints about 0.8 times as long as broad, terete; scape almost twice as long as wide, the apex slightly flaring (Fig. 8).

Thorax depressed and very long, almost three times as long as deep; mesonotum, scutellum and propodeum forming an even flat profile as does the mesosterum. Mesonotum and scutellum both strongly flattened but sloping down to the prescutellar scrobe; the latter a thin foveolate line curving anteriorly; notauli indicated only at the extreme base. Mesonotum, scutellum, mesosternum, most of pro- and meso-pleura highly polished, and sparsely, but rather coarsely, punctate; remainder of thorax and propodeum coriaceous-punctate. Propodeum long, evenly curved, and with only weak carinae; petiolarea and areola each about twice as long as wide; second lateral areas reaching far back toward hind coxae; carinae irregularly obscured apically.

Legs short and stout with polished, moderately coarsely punctate coxae; hind coxa bearing a small but sharp, nipple-like process subapically on the inner ventral surface.

Abdomen long and nearly parallel-sided, finely granular, with sparse, moderately coarse punctures basally on each tergite. Petiole short and broad. Gastrocoeli absent, thyridia large and conspicuous, interval about half as wide as the thyridia.

Black, with brown legs and the following brownish-yellow: flagellum, scape and pedicel below, mouthparts, clypeus, tegula, wing base, four anterior legs and trochanters more or less, third tarsus, thyridia, apical margins of tergites two to five.

Allotype, ♂.—Essentially like the female. Antennae longer, thinner, and thickly hairy; inner margins of eyes weakly convergent below; thorax and abdomen slightly slimmer, the propodeum noticeably thinner and slightly angular. Colored more brightly as follows: mouthparts, clypeus, scape and pedicel below, anterior margin of pronotum centrally, wing bases, tegula partly, four anterior legs in front and their coxae, except basally, bright yellow; apical margin of tergite two, and apical and basal margins of tergite three yellow.

Variation.—Females: flagellum 17- to 18-jointed. Hind legs brown to black; hind distitrochanter usually contrasting pale brown; abdominal tergites three and four often without contrasting pale margins.

Males; color of hind legs brown to black, anterior legs light to dark brown; four anterior coxae entirely, to only basally, brown; apical margins of the tergites from the second to the fourth, fifth or sixth, yellow to brown.

Cocoon.—Formed inside the host pupa.

Host.—Lepidopterous needle miners on lodgepole pine (*Pinus contorta* Douglas): in Alberta *Recurvaria starki* Freem., in California *Recurvaria milleri* Busck. Also reared from *Pinus jeffreyi* Grev. and Balf.

Specimens seen.—35 ♂ ♂ , 34 ♀ ♀ .

Holotype: Female, Sequoia National Park, California, Aug. 15, 1953, B. E. Wickham, reared from lodgepole pine needle miner, *Recurvaria milleri* Busck (Canadian National Collection No. 7057).

Allotype: Male, same data as holotype (C.N.C.).

Paratypes: CALIF., 2 ♂ ♂ , 1 ♀ , same data as holotype (C.N.C.); 2 ♂ ♂ , 3 ♀ ♀ , Yosemite, July 29 to Aug. 3, 1953, J. H. McLeod, reared from *R. milleri;* 8 ♂ ♂ , 13 ♀ ♀ , Lake Tenaya, Yosemite National Park, July 22 to Aug. 19, 1949, reared from *R. milleri* (C.N.C.); 6 ♂ ♂ , 6 ♀ ♀ , Tuolumne Meadows, Yosemite National Park, Aug. 3-31, 1957, G. R. Struble, reared from *R. milleri* (U.S.N.M.); 2 ♀ ♀ , Grant Grove, Sequoia National Park, July 29, 1957, S. Bechtal, reared from *Recurvaria* sp. (U.S.N.M.); 5 ♂ ♂ , 3 ♀ ♀ , Mammoth Lake district, Inyo National Forest, July 22, 1958, R. C. Hall, reared from *Pinus jeffreyi* (U.S.N.M.). ALTA., 2 ♂ ♂ , Banff, 1944, G. R. Hopping (C.N.C.); 2 ♂ ♂ , Upper Hotsprings, Banff, July 4-26, 1950 (C.N.C.); 1 ♂ , 2 ♀ ♀ , Hillsdale, Banff National Park, Aug. 18, 1949, K. Graham (C.N.C.); 1 ♂ , 1 ♀ , Banff, July 23-25, 1945, R. W. Stark and J. H. McLeod (C.N.C.); 1 ♂ , Mt. Eisenhower, Banff National Park, July 26, 1950 (C.N.C.); 1 ♂ , Mt. Girouard, Banff National Park, July 20, 1956, R. W. Stark (C.N.C.); 2 ♂ ♂ , 2 ♀ ♀ , Mt. Eisenhower, Banff National Park, July 27, 1956, R. W. Stark (C.N.C.); 1 ♂ , Jasper National Park, June 1954, R. W. Stark (C.N.C.). All Alberta specimens reared from *Recurvaria starki* Freem.

Summary

Three new parasitic Hymenoptera have been reared from the lodgepole pine needle miners *Recurvaria milleri* Busck in California and *R. starki* Freem. in Alberta. Two are Braconidae: *Meteorus pinifolii*, n. sp., and *Apanteles starki*, n. sp. The third, *Aethecerus pinifolii*, n. sp., belongs to a genus of Ichneumonidae long known from Europe but not previously recognized in North America.

On the Embryology of the Spruce Budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera, Tortricidae)[1]

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Introduction

Although the spruce budworm, *Choristoneura fumiferana* (Clemens), has received much attention as a result of its economic importance, little is known about its internal morphology and development. In this paper some features of the embryonic development will be described and compared with those of other Lepidoptera.

Materials and Methods

Eggs were reared at 25°C., fixed in Kahle's formo-acetic-alcohol for 24 hours, and preserved in 70 per cent alcohol. After storage in alcohol for more than a day most of the chorions could be removed without damaging the eggs. Both whole mounts and sections were prepared from this material.

TABLE I

SCHEDULE FOR EMBEDDING EGGS OF *C. fumiferana* AFTER THEY ARE FIXED IN
KAHLE'S ALCOHOLIC SOLUTION AND STORED IN 70 PER CENT ALCOHOL.

Step	1	2	3	4	5	6	7	8	9	10	11
Time (hours)	1	1	1	1	1	2	2	2	2	8	
	Per cent										
Water.	25	10	1	–	–	–	–	–	–	–	E
Ethyl alcohol.	50	40	24	5	–	–	–	–	–	–	M
N-Butyl alcohol.	25	50	75	95	100	75	50	25	–	–	B
Paraffin (56-58°C).	–	–	–	–	–	25	50	75	100	100	E
											D

Whole eggs, without their chorions, were stained overnight in Grenacher's alum carmine and then immersed in acidulated alcohol for half an hour to remove the stain from the yolk and leave the embryo bright red. The eggs were then washed in 95 per cent alcohol, cleared by cedarwood oil and mounted in thick Canada balsam. By using this technique it was possible to follow the external development and blastokinetic movements of the embryo.

For the preparation of sections, fixed, preserved eggs were infiltrated with and embedded in Fisher Tissuemat (56-58°C.) using essentially the same method as described by Smith (1943). The schedule is shown in Table I. Usually two or more eggs were orientated in different planes in the same block to provide a number of desired sections with on stroke of the microtome-knife. Heidenhain's iron haemotoxylin was used almost exclusively for staining sections. The following schedule was satisfactory: mordant in two per cent iron alum for three hours, stain for three to four hours, rinse in distilled water to remove the excess stain, differentiate in two per cent iron alum, and wash in tap water to blue the stain. Occasionally sections were counterstained with light green.

Results

The Egg at Oviposition

The egg at oviposition is 700μ long, 500μ wide and 200μ deep (Fig. 1). The chorion is transparent and about 3μ thick. Faint ridges of choriotic material radiate from the micropyle and the external surface of the egg is hexagonally sculptured (Fig. 2). Internally, the vitelline membrane lies between the chorion and the peripheral layer of cytoplasm. The periplasm is slightly vacuolate and slightly basophilic. It is from 6μ to 15μ thick. A fine network of cytoplasm connects the periplasm with the internal regions of the egg. Within this network yolk globules and particles constitute approximately 75 per cent of the volume of the oocyte (Fig. 3). The oocyte nucleus is in an island of cytoplasm near the dorsal side of the egg, midway between the anterior and posterior poles, and the spermatozoon is in a similar island immedaitely beneath the micropyle.

Cleavage

The meiotic division of the oocyte nucleus and the union of the sperm with the reduced nucleus to form the zygote nucleus occur during the first three hours after oviposition. The zygote nucleus then divides to form the first two cleavage nuclei. The number of primary nuclei is increased by nine synchronous cleavages of these two. The ninth cleavage occurs after many nuclei have entered the periplasm, following which cleavage is no longer synchronous.
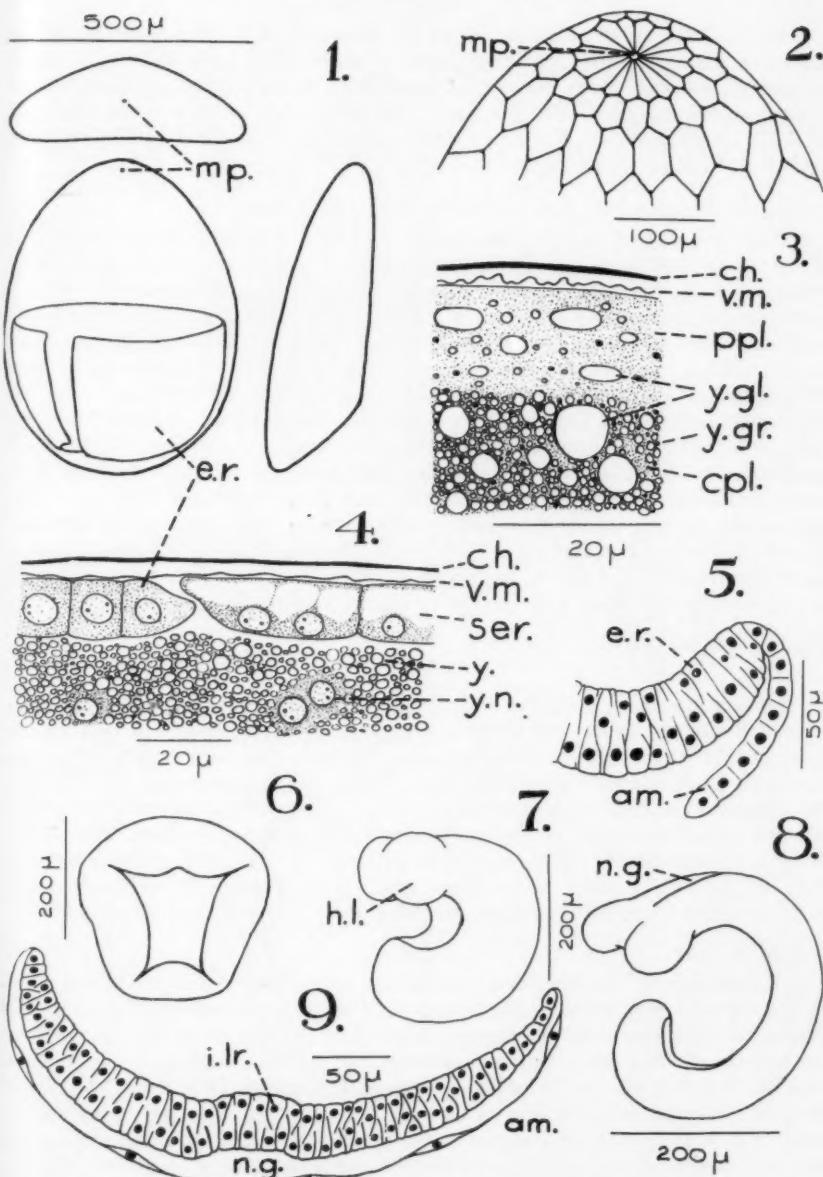
Figs. 1-9. 1, Dorsal, side, and end views of an egg of *C. fumiferana*. The early embryonic rudiment is shown in the dorsal view; 2, Antero-dorsal view of the external surface of the egg showing the micropyle and sculpturing; 3, Cross-section of part of the peripheral area of an egg at oviposition; 4, Cross-section of the blastoderm showing the serosa beginning to spread over the embryonic rudiment; 5, Cross-section of the embryonic rudiment showing the proliferation of the amnion; 6, External view of the embryonic rudiment; head lobes are toward the top of the page; 7, Dorsal view of egg showing the embryo at 19 hours; 8, The same at 21 hours; 9, Cross-section of a thoracic segment at 21 hours showing the inner layer beginning to invaginate.

By the fifth hour cleavage nuclei are arranged in a solid sphere near the center of the egg. This sphere of nuclei is about 200μ wide and its 32 nuclei are distributed uniformly, those on the perimeter of the sphere appearing similar to those in the anterior. There are no "cytopasmic tails" such as those described in other Lepidoptera by Eastham (1927), Gross and Howland (1940), Rempel (1951) and Presser and Rutsky (1957).

Formation of the Embryonic Rudiment and its Envelopes

Nuclei first reach the periplasm in the posterior region of the egg during the seventh hour, and by the eighth hour a superficial blastoderm is formed. Differentiation of this blastoderm into the serosa (outer embryonic envelope) and the embryonic rudiment begins during the ninth hour. The cells of the embryonic rudiment are mononucleate while the serosal cells are polynucleate and have large vacuolate areas along their proximal margins (Fig. 4). By the tenth hour differentiation is complete and the serosal cells have begun to spread over the embryonic rudiment. The serosa is completely formed by the eleventh hour; the cells merely flatten slightly and spread laterally until the embryonic rudiment is enclosed. At the same time the second embryonic envelope, the amnion, is being proliferated from the edges of the embryonic rudiment (Fig. 5). The cells of the amnion are mononucleate. They spread very thinly over the distal side of the rudiment separating it from the surrounding yolk; yolk contact is thus limited to the proximal side of the embryo. Both of these envelopes persist until the embryo is developed well enough to ingest them orally along with yolk.

### Development of the Embryo
10-23 hours

During the tenth hour the embryonic rudiment occupies most of the posterior half of egg and in the living egg it can be seen immediately beneath the transparent chorion and vitelline membrane (Fig. 1). By the thirteenth hour the rudiment has sunk into the yolk and is no longer visible externally. At this time the edges have folded inwards and the rudiment resembles a hollow pouch (Fig. 6). Its cells become increasingly columnar and compact and the head lobes become evident during the nineteenth hour (Fig. 7). There is a single layer of cells until about 23 hours; at this time a strip of cells along the mid-ventral side of the embryo invaginates to form the inner layer or mesoderm (Figs. 8, 9).

24-40 hours

As the cells of the inner layer divide and spread laterally to the dorsal edges of the embryo they form coelomic sacs, and at 40 hours two of these are well formed in each metamere or segment (Fig. 10). At the same time the embryo has become divided into seventeen segments, the cephalon or head at the anterior end and a telson or caudal pouch at the posterior end (Fig. 11). A pair of distinct coelomic sacs is found in each of the seventeen segments; they are indistinct in the cephalon and absent in the telson. The central nervous system is not well differentiated, the neuroblasts are proliferating cells (Fig. 10), and the gnathal and thoracic appendages are very similar, appearing as paired outgrowths from the ventral side of the embryo (Fig. 11).

41-80 hours

As development continues the gnathal appendages shift anteriorly and become grouped around the mouth, and any evidence of previous segmentation here is lost (Fig. 12). By 72 hours the labral lobes have fused and lie anterior to the mouth, while the maxillary and labial lobes are forming the spinneret posterior
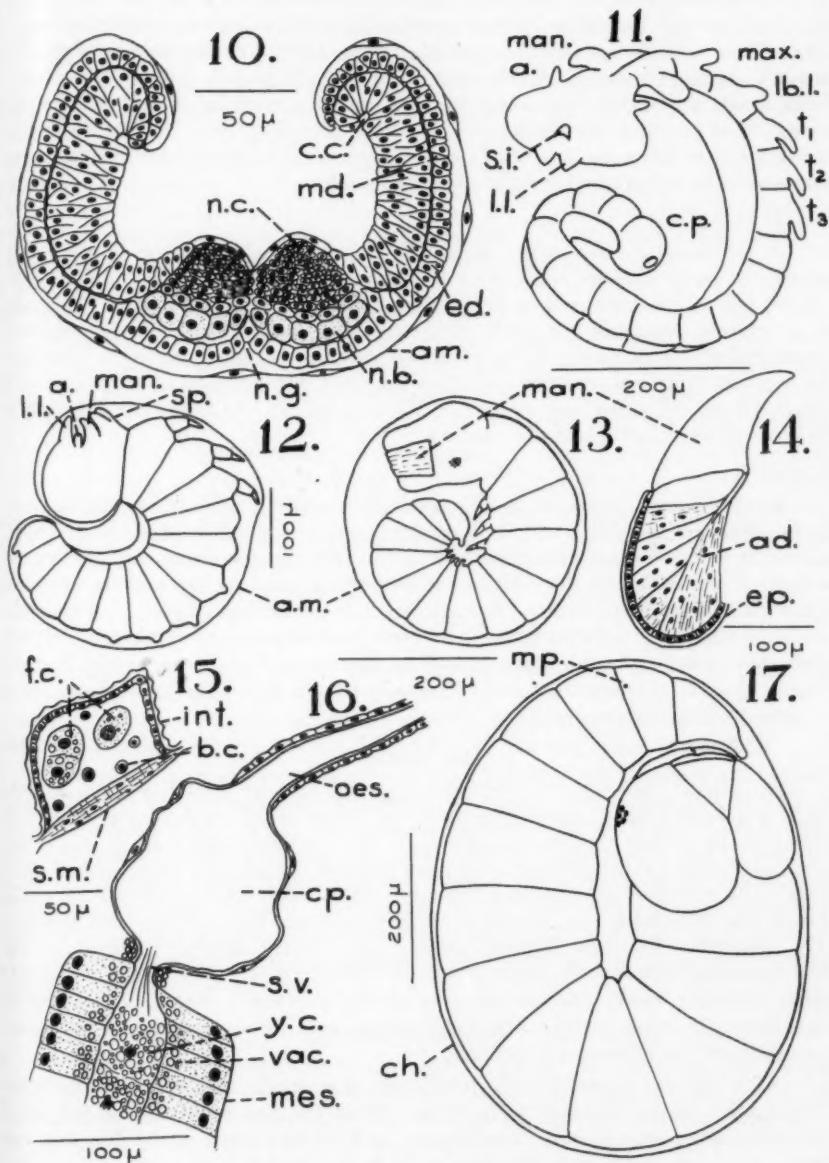
Figs. 10-17. 10, Cross-section of an abdominal segment at 40 hours; 11, External appearance of the embryo at 40 hours; 12, The same at 72 hours; 13, The same at 100 hours; 14, Cross-section of the adductor muscle of the sclerotized mandible at 100 hours; 15, Longitudinal section of a portion of an abdominal segment at 100 hours; 16, Longitudinal section of the stomodaeum and mesenteron at 100 hours; 17, Mature embryo (150 hours) about to hatch.

to it. The mandibles are lateral to the mouth, the antennae lie just dorsad of the bases of the mandibles, paired appendages are evident on abdominal segments three, four, five, six and ten, and the lateral walls of the embryo have grown dorsally nearly closing along the mid-dorsal line (Fig. 12). Within the next eight hours the walls close along this line and the embryo rotates around its longitudinal axis through 180 degrees (blastokinesis) (Fig. 13). Following dorsal closure the embryo no longer absorbs Grenacher's alum carmine because the ectodermal cells have begun to secrete the cuticle.

81-150 hours

At 96 hours the mandibles are the only sclerotized structures and by 100 hours the body muscles, stomodaeum and mesenteron appear functional (Fig. 14, 15, 16). The embryo soon breaks through the amniotic sac and at 120 hours it is actively ingesting the yolk which fills the anterior half of the egg; all development has occurred in the posterior part of the egg until now. Within the next 24 hours the embryo consumes the yolk and embryonic envelopes and grows to fill the entire egg (Fig. 17). It emerges at 150 hours by chewing a hole in the anterior end of the chorion.

Blastokinesis

By 16 hours the embryo has begun to rotate either to the right or left around its longitudinal axis (Figs. 6, 7). It is not possible to predict which way it will turn, but equal numbers turn in each direction (the illustrations are of an embryo which turned left). In three hours this movement is completed and the embryo lies with its head lobes directed towards one side of the egg (Fig. 7). It remains in this position for about 60 hours. At the end of this time the walls have closed dorsally and the embryo rotates around its longitudinal axis through 180 degrees (Figs. 12, 13). Finally, between 130 and 144 hours it rotates 45 degrees, again around its longitudinal axis (Fig. 17).

Discussion

In general, spherical or ellipsoidal eggs are best for embryological studies and, as a result, most of the embryological information on insects is based on those species having regularly-shaped eggs. In the Lepidoptera, members of the families Pieridae and Pholaenidae and the genus *Bombyx* have subspherical eggs, hence the embryology of these groups is fairly well known (Eastham, 1927; Gross and Howland, 1940; Hensen, 1932; Johannsen, 1929; Presser and Rutsky, 1957; Rempel, 1951; and Toyama, 1902). The Tortricidae, whose eggs are flat and scalelike, have received little attention (Huie, 1918). Their eggs are essentially two-dimensional and the embryos do not develop as regularly as those in spherical eggs, consequently, orientation of the eggs for sectioning and the interpretation of the sections are difficult.

Although development in *C. fumiferana* is generally similar to that in other Lepidoptera, two differences were noted. First, the cleavage nuclei do not form a hollow sphere nor possess "cytoplasmic tails" as described in the Pieridae and Phalaenidae (Eastham, 1927; Rempel, 1951; Presser and Rutsky, 1957). Secondly, during dorsal closure of the embryo very little yolk is enclosed in the mesenteron.

Observations suggest that migration of cleavage nuclei in this species is controlled to some extent by the mitotic forces which operate during cleavage. The mitotic spindles are not regularly oriented in relation to the surface of the egg and at each cleavage the daughter nuclei move into the most easily filled spaces. As a result a solid sphere of cleavage nuclei develops and, as the size of the sphere

increases, the peripheral nuclei enter the periplasm to form the blastoderm while the interior ones remain in the yolk to form the yolk cells.

In the other Lepidoptera studied most of the yolk is enclosed in the mesenteron as the lateral walls of the embryo grow dorsally, but in *C. fumiferana* very little yolk is enclosed in this way; most of it is orally ingested by the embryo between 120 and 144 hours. At 100 hours, although the embryo is still small and confined to the posterior half of the egg, its cuticle has been secreted, its muscles, stomodaeum, and mesenteron appear functional and its mandibles are sclerotized (Figs. 12, 13, 14). The shape of the egg may govern this unusual mode of yolk consumption; it may be difficult for the embryo to enclose most of the yolk and develop successfully in such a disc-shaped egg.

Summary

The egg at oviposition is disc-shaped, 700μ long, 500μ wide and 200μ deep. The chorion is 3μ thick and has a single micropyle. A vitelline membrane separates the chorion from the cytoplasm which is divided into a peripheral periplasm and an internal cytoplasmic network surrounding the yolk globules.

The zygote nucleus is formed during the first three hours after oviposition. Then cleavage begins and continues synchronously for five hours (at $25°C.$). The nuclei have no "cytoplasmic tails" and do not form a hollow sphere as they move from the centre of the egg to the periplasm. At each cleavage the daughter nuclei occupy the most easily filled spaces; as a result a solid sphere of nuclei develops and only the peripheral of these enter the periplasm to form the blastoderm. The remaining nuclei form yolk cells. Migration of cleavage nuclei in this species is probably controlled to some extent by mitotic forces.

A superficial blastoderm is formed by eight hours and differentiation into serosa and embryonic rudiment is complete in two hours. The serosa spreads over the embryonic rudiment and is complete at 11 hours. At the same time the amnion is being proliferated from the edges of the embryonic rudiment.

Invagination of the mesoderm begins at 23 hours and segmentation is complete at 40 hours. Dorsal closure occurs at about 80 hours and blastokenesis follows immediately. Then the cuticle is secreted. By 96 hours the mandibles are sclerotized and by 100 hours the body muscles, stomodaeum and mesenteron appear functional. At 120 hours the embryo has broken through the amnion and is actively ingesting the yolk. It consumes all the yolk and embryonic envelopes, grows to fill the egg completely and emerges at 150 hours. Oral consumption of so much yolk is unusual among Lepidoptera but in this species it may be necessary because of the disc-shaped egg.

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Abbreviations Used in Figures

a. antenna; am. amnion; ad. adductor muscle of mandible; b.c. blood cell; c.c. coelomic sac; ch. chorion; cp. crop; cpl. cytoplasm; c.p. caudal pouch; ed. epidermal layer; ep. epidermis; e.r. embryonic rudiment; f.c. fat cell; h.l. head lobe; i.lr. inner layer; int. integument; lb.l. labial lobe; l.l. labral lobe; man. mandible; md. mesoderm; mes. mesenteron; mp. micropyle; n.b. neuroblast; n.c. neural cells; n.g. neural groove; oes. oesophagus; ppl. periplasm; ser. serosa; s.i. stomodaeal invagination; s.m. segmental muscle; sp. spinnerette; s.v. stomodaeal valve; t1,2,3. thoracic segments 1,2,3; vac. vacuoles; v.m. vitelline membrane; y. yolk; y.c. yolk cell; y.n. yolk nucleus.

Observations on the Life History, Distribution, and Abundance of Two Species of *Cecidomyia* (Diptera, Cecidomyiidae) on Jack Pine in Manitoba and Saskatchewan[1]

By W. A. REEKS[2]

Introduction

The occurrence of midges on jack pine, *Pinus banksiana* Lamb., in Manitoba has been reported by Lejeune (4), Barker and Wong (1), and Prentice and Hildahl (5, 6). The Forest Insect Survey also reported a species of *Retinodiplosis* on jack pine in Ontario, and Barnes (2) suggested that this may have been *R. resinicola* (Osten Sacken). This name was also provisionally assigned to a species found near Stead, Manitoba, in 1956 (7). Vockeroth (8) now shows that *Retinodiplosis* Kieffer is a synonym of *Cecidomyia* Meigen, which is represented by at least two species on jack pine in Manitoba and Saskatchewan. These are *C. reeksi* and *C. banksianae*. The former is the more common and undoubtedly was the species most frequently represented in the early reports of pine midges in Manitoba.

Infestations of pitch midges on jack pine were encountered near Stead and Belair, Manitoba, in 1956. The Forest Insect Survey followed the progress of these until populations declined to a very low level in 1958. The present paper is a summary of observations, collections, and rearings of midges during this three-year period.

Cecidomyia reeksi Vockeroth

Life History

This midge undergoes one generation a year in Manitoba. The oviposition period is short, and its beginning coincides with the peak of pollination of jack pine. Eggs were found in the field on May 19 in 1956, June 3 to 12 in 1957, and May 30 to June 5 in 1958. The eggs are laid singly on the bark of the current shoots, on the new needles, or at the axis of the needle bundle and current shoot. They are never found on fresh pitch masses. It is questionable if adults are attracted to the most resinous shoots for oviposition. Fifty shoots each of field-collected "lightly resinous" (zero to three globules of pitch per shoot) and "very resinous" (over five globules of pitch per shoot) shoots showed that 26 per cent of the former and 39 per cent of the latter supported eggs on oviposition sites. Females of 27 paired adults in cages under insectary conditions laid from one to 23 eggs, but the potential egg production probably is greater than these figures indicate. The incubation period is about six days.

After hatching, the young larvae crawl to pitch masses on the current shoots and embed themselves in the pitch. The feeding habits of the midge and the cause of pitch flow from infested shoots are in doubt. In discussing the method of feeding of *Cecidomyia résinicola* (O.S.) (= *Diplosis resinicola*), Eckel (3) noted that the masses of soft resin contained microscopic splinters of wood fibre. She suggested that these wood particles may have been separated from the plant by the twisting of the young spiny larvae, which in some cases made a slight concavity in the cambial area under the pitch masses. She could find no evidence of woody tissue in the digestive tract, which implies that resin and not plant tissue is the food material of *C. resinicola*. Certain similarities were noted in the present study. When larvae first inhabit the pitch mass there is evidence of cambial injury at the source of the resin. Injury to the cambium is more noticeable as the larvae develop. This is associated with red staining of the resin near the larvae or with minute particles resembling red bark tissue floating free in the pitch. *C. reeksi* has greatly reduced mouth parts, presumably inadequate for rasping plant tissue, and it lacks a spatula, which is said to be used by some species for tearing plant tissue. It is believed that the larvae of *C. reeksi* feed on resin, a flow of which may be ensured by injury to the cambial area. The injury is perhaps mechanical, or possibly it is caused by enzymatic action of extra-intestinal digestion as in the case of another cecidomyid, *Miaster* sp. (9).

The insect passes the winter as a partially grown larva, not in a cocoon as forecast in an earlier report (7). By spring the infested pitch mass is heavily encrusted and darkened, but still shows a tinge of yellow from the embedded larvae. The resumption of feeding in the spring appears to be associated with a renewal of resin-flow, which enlarges the pitch mass, and there is some evidence of at least one larval moult in the spring. Pupae are found throughout most of May (Table I) within the pitch masses. Following adult emergence, the empty pupal cases remain half protruding from the pitch masses (Fig. 1). These first appear in field collections about May 21 (Table I) and emergence is finished by June 5. The emergence period closely coincides with pollination of jack pine. Under insectary conditions, the mean emergence dates were May 26 and May 27 for males and females, respectively, in 1957, and May 20 and May 21 in 1958. Of the 210 specimens reared, 92 were males and 118 were females. Both males and females lived from one to six days in the insectary, with an average of three for males and four for females.

TABLE I

Spring Development of *C. reeksi* based on Collections of Living Material in Pitch Masses
on One-year old Shoots of jack pine at Belair, Manitoba

Date	1957				1958			
	No. collected	Per cent by stages			No. collected	Per cent by stages		
		Larvae	Pupae	Adults		Larvae	Pupae	Adults
Apr. 16	–	–	–	–	117	100	0	0
Apr. 24	44	100	0	0	73	100	0	0
May 6, 7	61	73	27	0	32	100	0	0
May 10–14	96	52	48	0	31	68	32	0
May 16	95	22	78	0	–	–	–	–
May 21–23	85	0	100	0	4	25	50	25
May 28–30	46	2	28	70	0	0	0	0
June 3– 5	47	3	3	98	–	–	–	–

Note: Adults refer to empty pupal cases.

Mortality

The insect presumably is vulnerable to attack by predators in June during
the egg stage and while the first instar larvae migrate to pitch masses, but data
on mortality during this vulnerable period are lacking. The cumulative mor-
tality from the end of June to May of the following year is easily determined by
examining the contents of infested pitch masses (Table II).

Two important causes of mortality whilst the insect is in the pitch mass
are parasites and weather.

The most common parasite is an endoparasite of the tribe Pteromalini.
Unfortunately, the specimens reared were males, and according to Dr. O. Peck,
Entomology Research Institute, Department of Agriculture, Ottawa, females are
essential for identification. The degree of parasitism of larvae by this species
was not determined, but its effectiveness some years is apparent by examining

TABLE II

Mortality and Survival *C. reeksi* based on Dissections of 273 Field-collected Pitch Masses
in 1957 and 310 in 1958 at Belair, Manitoba

Year and Month	Total Midges	Per cent midges collected as						Emerged adults
		Larvae			Pupae			
		Living	Dead	Parasitized	Living	Dead	Parasitized	
1957								
April	61	72	28	0	0	0	0	0
May	634	21	34	0	39	6	0	0
June	118	0	40	0	2	0	20	38
1958								
April	247	77	23	0	0	0	0	0
May	387	14	81	1	3	0	0	1
June	157	0	100	0	0	0	0	0

Parasitized larvae refer to ectoparasites only; parasitism of living larvae by endoparasites not
determined.
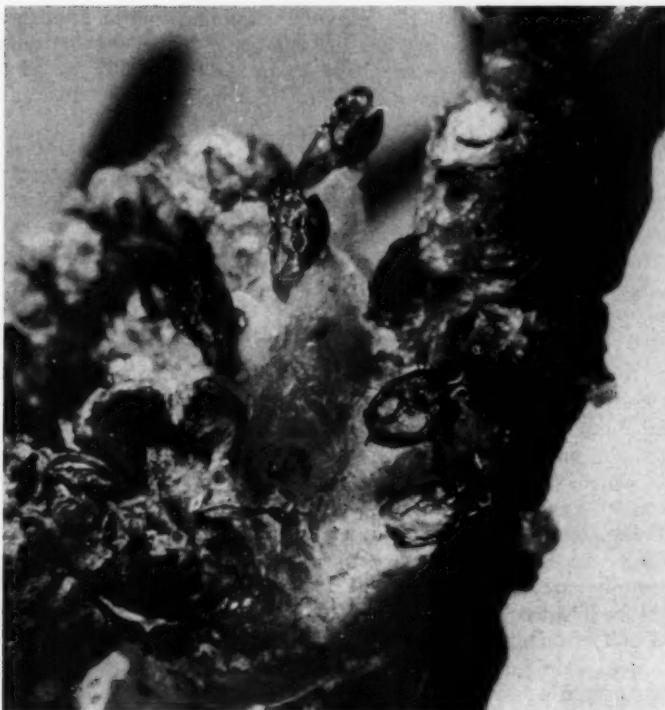
Fig. 1. A pitch mass on a year-old shoot of jack pine showing empty pupal cases of *Cecidomyia reeksi*.

the June collections of 1957 (Table II). Of the 118 living and dead midges dissected from pitch masses, 20 per cent were parasitized in the pupal stage. Effective parasitism was negligible in 1958 because most of the midge material died in the larval stage from other causes. A very small number of undetermined chalcidoid ectoparasites were also encountered but not reared to the adult stage.

The cumulative larval mortality is high every spring, but it was especially high in the spring of 1958. All field collections after May 1, 1958, showed larval mortality ranging from about 80 per cent to 100 per cent (Table II), whereas a check lot of 30 infested shoots collected on April 24 and reared in the insectary showed only 10 per cent mortality. Larval mortality in the spring is accompanied by drying of the pitch masses. It is often questionable if the killing of larvae by weather or other factors is responsible for the cessation of resin flow and subsequent hardening of the pitch masses, or if some aspect of weather retards the resin flow, causing the pitch masses to harden and the larvae to die. The weather of 1958 undoubtedly had both an indirect and direct effect in the killing of larvae. A severe case of "winter-drying" caused many infested jack pine shoots to die or desiccate to the point where there was little or no resin flow. This condition was followed on April 28 and 29 by extremely low temperatures, which at Winnipeg were 8.4°F. and 7.4°F., respectively. It was probably the combined effect of these two weather conditions that caused the

high mortality shown in Table II. Survival of midges within pitch masses was 38 per cent in 1957 and less than one per cent in 1958. Total mortality to the spring of 1958 reduced populations of adults to the extent that the next generation occurred only in endemic numbers in the principal study area at Belair.

Abundance

The abundance of the insect is governed by the number of insects in a pitch mass, the number of infested pitch masses on a shoot, and the proportion of infested shoots on a tree.

Periodic collections at Belair consisted of 200 infested shoots each year. The number of midges in a pitch mass ranged from one to 13, with a mode of one and an average of three in 1957 and 1958. The number of pitch masses per infested shoot ranged from one to seven, with a mode of one each year.

Four trees were sampled for three consecutive years at Belair, where the heaviest known infestation occurred in Manitoba. Objectives were to learn something about the distribution of infested pitch masses in the tree crown and annual changes in the proportions of current shoots attacked by the midge. The trees were 25 years old in 1956. They were slow growing, and had been attacked in 1954 and 1955 by the jack pine budworm, *Choristoneura pinus* Free. Sample branches were permanently marked but not cut, and totalled four from each of three crown levels of each sample tree. The current shoots on each branch were counted at the end of the growing season (while the current shoots could still be distinguished from the older ones). The branches were again examined in October for counts of infested current shoots. The percentage of current shoots infested by midges was then recorded. The percentages were then transformed by angular transformation, and analyses of variance were applied to show something of the inter-tree and intra-tree variability. Significant differences were evident only in 1957, when populations were high. That year percentages of current shoots attacked were significantly different between levels (F=5.67 with two and 36 degrees of freedom). However, the tree-by-crown level interaction was also significant (F=3.27 with six and 36 degrees of freedom), indicating that differences by crown levels were not consistent between trees. The results of the sampling are shown as actual percentages in Table III. It is clear that the intensity of the infestation declined in 1958, when only about one per cent of the current shoots were attacked. Incidental information from the shoot counts show that there is not always a progressive increase in the annual production of new shoots. The number of new shoots may decline from the previous year. This happened in 1957, which was a year of very high flower production. Under this condition, production of new shoots is light in the inner crown and many of the old terminals die from suppression.

Damage

Of 408 tagged shoots that were attacked in 1957, 75 per cent were dead the following summer and showed evidence of injury to the cambium under the pitch masses. It is therefore considered that the midge is primary and capable of killing shoots, but the degree of shoot-killing is not considered serious in the Prairie Provinces. The largest and most severe infestation in Manitoba covered an area of about two square miles in 1957. Even when these trees in the Belair area showed about 15 per cent infestation of the shoots, the effect on increment was negligible. However, infested trees were still showing the effects of earlier budworm defoliation. The heaviest infestations on older trees

TABLE III

Percentage of Current Shoots of jack pine attacked by *C. reeksi* at Belair, Manitoba.
Shoots counted on twelve branches on each of four trees.

Crown level	Total current shoots			Per Cent current shoots attacked		
	1956	1957	1958	1956	1957	1958
Upper................	691	556	718	10.4	13.6	2.2
Middle...............	1,809	1,064	1,372	6.0	18.7	1.2
Lower................	2,323	1,232	1,412	7.2	10.8	1.1
Total................	4,823	2,852	3,502	7.2	14.4	1.3

appear to occur on open growing trees on poor sites, conditions similar to those that are attractive to the budworm.

The most important known damage is to young reproduction, which is occasionally killed outright and often damaged to the extent of killing leaders and branches.

Distribution

From 1956 to 1958 the Forest Insect Survey collected *C. reeksi* at 20 locations in Manitoba and Saskatchewan. It was taken within the full range of sampling from the Ontario border to The Pas in Manitoba, and to Lac La Ronge and Buckland in Saskatchewan. Specimens collected by Dr. J. B. Thomas show that the species is present at Black Sturgeon Lake, Ontario. The distribution of the insect probably covers most of the range of jack pine.

Cecidomyia banksianae Vockeroth

Observations on this species were confined to a very small amount of material associated with collections of *C. reeksi*.

Field observations and rearings show that eggs are laid singly on the needles or bark close to terminal buds. They are found from about June 12 to 24. The movement of newly emerged larvae to feeding sites was not observed. The winter is passed in the larval stage. By late April the larvae are embedded in the meristematic tissue near the base of the bud or developing shoot, and the cavity becomes filled with resin. Infested shoots may contain one to eleven larvae, but one is the usual number. The larvae start to issue from the cavities in early May, and crawl to needles or bark of year-old shoots for cocoon spinning. Pupation occurs within the whitish cocoon, which can be found from about May 10 to May 24 in the Belair area. Under insectary conditions in 1957, the mean emergence dates for males and females were May 30 and June 1, respectively, with the total emergence period ranging from May 27 to June 4. Emergence of *C. banksianae* was about four or five days later than that of *C. reeksi* reared under identical conditions. Of the 30 specimens successfully reared to the adult stage, 12 were males and 18 were females.

C. banksianae, although rare, has been collected at eight locations in Manitoba and Saskatchewan, and occurs as far east as Black Sturgeon Lake in Ontario. Its full range of distribution is unknown.

Infested buds or overwintering shoots may start to die by May 10. Less seriously mined shoots may continue to grow to about mid-June or until they attain a length of up to two inches. Affected buds or shoots bend obtusely at the point of injury. The insect is not known to be of economic importance in the Prairie Provinces.

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